

THE FOSSIL BIRDS OF THE LATE MIocene AND EARLY PLIOCENE
OF FLORIDA

BY

JONATHAN J. BECKER

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1985

Copyright 1985

by

Jonathan J. Becker

ACKNOWLEDGMENTS

I would first like to thank my advisor, Pierce Brodkorb, for his support, guidance, and friendship during the course of this project. He has provided much encouragement and council throughout my researches on fossil birds, as have the members of my committee--Drs. Richard A. Kiltie, S. David Webb, Elizabeth S. Wing, and Ronald G. Wolff. I thank them for the many hours spent reading this manuscript and for their many helpful comments pertaining to my research.

A number of friends and colleagues contributed to this study with their comments, suggestions, and discussions. They include S. Emslie, R. Hulbert, and A. Pratt. Gary S. Morgan has taken much time to discuss the geology of Florida and systematics, evolution, and biochronology of fossil and Recent mammals, in addition to many other aspects of vertebrate paleontology. I especially thank him for his comments on Chapter III. Storrs Olson has freely shared his considerable knowledge and insights of avian systematics, evolution and anatomy. David Steadman also provided many helpful comments. I also thank Cynthia West for her support and aid in completing this dissertation.

I thank the many amateur fossil collectors who have generously donated fossil birds from the included localities to the Florida State Museum. They include Danny Bryant, George Hesslop, and Ron Love. Phil Whisler, of Venice, Florida, originally discovered the SR-64 locality and brought it to the attention of the staff of the Florida State Museum. Rick Carter, of Lakeland, Florida, deserves special mention, for over the

last three years, he has donated hundreds of specimens of fossil birds from the Bone Valley Mining District to the Florida State Museum. Without his generous contributions, the Bone Valley portion of this study would have been impossible to complete. John Waldrop is also gratefully acknowledged for providing information about the avian localities in the Bone Valley.

I also thank the following individuals and institutions for making fossil and/or Recent specimens available for study: A. Andors, G. Barrowclough, C. Houlton, R. H. Tedford, F. Vuilleumier, American Museum of Natural History; P. Brodkorb, Department of Zoology, University of Florida; J. Chenval, C. Mourer, Universite Claude Bernard; J. Hardy, B. J. MacFadden, G. S. Morgan, S. D. Webb, T. Webber, Florida State Museum; R. Mengel, University of Kansas; R. Payne, University of Michigan; M. Voorhies, University of Nebraska; H. James, S. L. Olson, D. Steadman, United States National Museum. Helen James, Storrs L. Olson, and David Steadman generously provided accommodations during a lengthy stay in Washington, D.C.

Financial support received while at the University of Florida, includes teaching and research assistantships from the Department of Zoology, College of Liberal Arts and Sciences; teaching assistantships from the Department of Physiological Sciences, College of Veterinary Medicine; a curatorial assistantship from the Department of Vertebrate Paleontology, Florida State Museum; and grants from the Frank M. Chapman Memorial Fund, American Museum of Natural History, and from Sigma Xi Grants-In-Aid of research. The Department of Zoology, College of Liberal Arts and Sciences, and the Florida State Museum supplied all expendable

equipment. I gratefully acknowledge these departments and institutions for their support.

Last, I thank my parents, Elwood W. and Nita E. Becker, for their encouragement and support over the years. They have provided not only the opportunity, but much of the impetus, that has allowed me to finish my formal education.

TABLE OF CONTENTS

	PAGE
ACKNOWLEDGMENTS	iii
ABSTRACT	viii
CHAPTER	
I. INTRODUCTION AND PREVIOUS WORK	1
Introduction	1
Limitations of Study	2
Previous Work	4
II. METHODS	9
Measurements	9
Computer Software	18
Nomenclature	18
Systematics	27
Paleoecology	27
Biochronology and Faunal Dynamics	27
Specimens Examined	29
Abbreviations	29
III. GEOLOGY	31
Biochronology	31
Local Faunas	33
Eustatic Sea-level Changes	41
IV. SYSTEMATIC PALEONTOLOGY	49
Order Podicipediformes	49
Order Pelecaniformes	65
Order Ciconiiformes	90
Order Accipitriformes	116
Order Anseriformes	136
Order Galliformes	155
Order Ralliformes	158
Order Charadriiformes	175
Order Strigiformes	191
Order Passeriformes	195

V. PALEOECOLOGY	198
Introduction	198
Local Faunas	199
VI. BIOCHRONOLOGY AND FAUNAL DYNAMICS	205
Introduction	205
Faunal Dynamics	205
Biochronology	213
VII. SUMMARY	224
Systematics	224
Paleoecology	227
Biochronology	228
LITERATURE CITED	229
BIOGRAPHICAL SKETCH	245

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

THE FOSSIL BIRDS FROM THE LATE MIocene AND EARLY PLIOCENE
OF FLORIDA

By

Jonathan J. Becker

August 1985

Chairman: Pierce Brodkorb

Major Department: Zoology

This study examined the non-marine avifauna from ten late Miocene and early Pliocene localities in Florida. These localities include the Love Bone Bed, McGehee Farm, Mixson's Bone Bed, Bone Valley Mining District, Withlacoochee River 4A, Manatee County Dam, SR-64, Haile VB, Haile VI, and Haile XIXA. Non-marine genera (number species, if more than one) present include Rollandia, Tachybaptus, Podilymbus (2), Podiceps, Pliodutes, Phalacrocorax (3), Anhinga (2), Ardea (2), Egretta (2 or 3), Ardeola, Nycticorax, Mycteria, Ciconia (3), Eudocimus, Plegadis, Threskiornithinae, genus indeterminate, Pliogyps, Pandion (2), Haliaeetus, Buteo, Aquila, Accipitrid, genus indeterminate (3), Dendrocygna, Branta, Anserinae, genus indeterminate (4), Tadorine, genus indeterminate, Anas (2), Anatine, genus indeterminate (2), Aythya, Oxyura, Meleagridinae, genus indeterminate, Meleagris, Grus (2), Balearicinae, genus indeterminate, Aramornis, Rallus (3), Rallid, undescribed genus, Phoenicopterus (2), Jacana, Limosa, "Calidris" (6+),

?*Actitis*, ?*Arenaria*, ?*Philomachus*, Tytonid, undescribed genus, Bubo,
Passeriformes (2).

The largest avifaunas are from the Love Bone Bed local fauna (44 taxa present) and the Bone Valley local fauna (41 taxa present, 31 here included). These two localities are the most diverse non-marine and marine avifaunas, respectively, known in North America prior to the Pleistocene.

An analysis of the faunal dynamics of the Neogene fossil birds from North America shows the following results. (1) Localities which have produced fossil birds are not uniformly distributed through time--74.4% of the localities are from the last 41% of the Neogene. (2) By the Barstovian, a majority of the living families which have a fossil record, have appeared. (3) Generic diversity increases from 10 to 98 during the Neogene. (4) The marine avifauna is essentially established at a diversity of 20 to 25 genera by the Clarendonian. (5) The non-marine avifauna increases continually throughout the Neogene. (6) Origination rates for marine birds peak in the Clarendonian with 4.4 genera appearing per million years. (7) Extinction rates for marine birds are consistently low throughout the Neogene. (8) Origination rates for non-marine birds show a 2- to 4-fold increase in alternate Land Mammal Ages. (9) Turnover rates parallel the origination rates described above.

CHAPTER I
INTRODUCTION AND PREVIOUS WORK

Introduction

Florida has one of the richest records of fossil birds in the world. This study examines the systematics of the non-marine fossil birds which lived in Florida during the late Miocene and early Pliocene (9.0--4.5 million years before present) and the paleoecology of the localities which produced them. Included is material from 10 local faunas--the Love Bone Bed, McGehee Farm, Mixson Bone Bed, Bone Valley, Withlacoochee River 4A, Manatee County Dam Site, SR-64, Haile VB, Haile VI, and Haile XIXA. Only a few of the birds from McGehee Farm and the early collections of birds from Bone Valley have been studied previously (Table 1.1). In addition, the biochronology and faunal dynamics of the entire North American Neogene avifauna are investigated. Specifically, the following questions are addressed:

Systematics

1. What species of fossil birds are present in Florida during the late Miocene and early Pliocene?
2. What are their systematic and biogeographic relationships to other fossil and Recent species?

Paleoecology

1. Can fossil birds be used to reconstruct the paleoenvironments of the fossil localities examined in this study?

Biochronology and Faunal Dynamics

1. What is the temporal distribution of the fossil localities producing birds in the Neogene of North America?
2. What is the temporal distribution of the North American Neogene avifauna?
3. When, and at what rate, do the North American Neogene avian families and genera appear and become extinct?
4. How do the marine and non-marine localities and avifaunas differ in questions 1 to 3 above?
5. What avian species are biostratigraphically useful in the Neogene of North America?
6. What degree of temporal resolution does avian biochronology offer?

Limitations of Study.

There have been several limitations imposed on this study by the current knowledge of avian systematics and paleontology, and to a lesser degree by the lack of previous studies dealing with the paleoecology and biochronology of birds. Birds are often considered ". . . the best known and most completely described class of animals . . ." (Welty 1975:14). In reality, this statement applies only to the simple designation of living forms and to the obvious aspects of their behavior and ecology, but definitely not to their evolution, their superspecific relationships, and to many aspects of internal morphology. Many living groups of birds still lack modern systematic revisions based on internal morphology, or in many, even a description of their internal morphology. Most modern orders have never been shown to be monophyletic, although many are doubtlessly so. Modern classifications of birds above the specific level

(e.g., American Ornithologists' Union, 1983) has changed very little in the 90 years since Gadow's (1893) classification. Olson (1981a:193), addressing this problem, states

Many ornithologists appear to believe that the higher-level systematics of birds is a closed book, the sequence of orders and families in their field guides being an immutable constant that was determined long ago according to some infallible principle. In reality, the present classification of birds amounts to little more than superstition and bears about as much relationship to a true phylogeny of the Class Aves as Greek mythology does to the theory of relativity. A glance at the Gadow-Wetmore classification now in use shows that there is still no concept in ornithology of what constitutes a primitive bird.

Certainly correct phylogenies are impossible to develop without an accurate knowledge of primitive character states, the distribution of primitive and derived characters within the group being studied, and meaningful outgroup comparisons.

Many fossil species are described from single, non-diagnostic elements, making useful comparisons between, or among, species impossible. But even diagnostic elements, when singly preserved, add little to our understanding of the phylogeny and evolution of that taxon. Other species are arbitrarily allied with the wrong family, the wrong order, and even in some cases, with the wrong class of vertebrates (cited in Brodkorb, 1978:211-228), many because of lack of proper comparisons. Only recently have many of these errors been recognized, due in part to an increased number of workers in the field, and from greater availability and use of comparative skeletal material. Adequate skeletal collections are still lacking for many common species (Zusi et al., 1982).

It is outside the scope of this study to revise the many recent and fossil genera and families which need such treatment. In such cases, I

try to note the systematic problems in each group, briefly review its fossil record, and describe the fossil material from Florida. This material should be reexamined as the state of systematics of these groups improves and as additional Recent and fossil material becomes available.

Previous Work

The earliest published report of fossil birds from Florida is Sellard's (1916) description of a supposed jabiru (Jabiru? weilli =Ciconia maltha) from Vero, closely followed by Shufeldt's (1917a, 1917b) study of this local fauna. Wetmore (1931) reviewed the Pleistocene avifauna of Florida and was also the first to report (1943) on the Tertiary birds from Thomas Farm and the Bone Valley Mining District. Numerous studies have appeared since then, primarily by Brodkorb or his students. A few other faunal and systematic studies have also included avian material from Florida.

Table 1.1 lists many of the fossil localities in Florida which have a notable record of fossil birds. Reference to Brodkorb's Catalogue of Fossil Birds (1963-1978), where the avifaunas from many Florida Pleistocene localities were first reported, is omitted to conserve space.

Table 1.1. Avian Fossil Localities of Florida.

<u>Locality</u>	<u>Reference (s)</u>
<u>MIocene TO EARLIEST PLIOCENE (Pre-Blancan)</u>	
Bone Valley, Polk Co.	Becker, 1985a; Brodkorb, 1953b, 1953c, 1953d, 1953e, 1955a, 1970; Olson, 1981b; Steadman, 1980; Wetmore, 1943; this study
Gainesville Creeks, Alachua Co.	Brodkorb, 1963b
Haile VI, Alachua Co.	Brodkorb, 1963a; this study
Haile XIXA, Alachua Co.	this study
Love Bone Bed, Alachua Co.	Becker, 1985a, 1985b; Webb et al., 1981; this study
Manatee Co. Dam Site Manatee Co.	Webb and Tessman, 1968; this study
McGehee Farm, Alachua Co.	Brodkorb, 1963a; Hirschfeld and Webb, 1968; Olson 1976; this study
Mixson Bone Bed, Levy Co.	this study
Seaboard Airline Railroad, Leon Co.	Brodkorb, 1963b
SR-64, Manatee Co.	this study
Thomas Farm, Gilchrist Co.	Brodkorb, 1954a, 1956a, 1963b; Cracraft, 1971; Olson and Farrand, 1974; Steadman, 1980; Wetmore, 1943, 1958
Withlacoochee River 4A, Marion Co.	Becker, 1985a; this study
<u>LATE PLIOCENE (Blancan)</u>	
Haile XVA, Alachua Co.	Campbell, 1976; Steadman, 1980
Santa Fe IB, Gilchrist Co.	Brodkorb, 1963d

Table 1.1--continued.

<u>Locality</u>	<u>Reference (s)</u>
<u>EARLY PLEISTOCENE (Irvingtonian)</u>	
Coleman IIA, Sumter Co.	Ritchie 1980; Steadman, 1980
Haile XVIIA, Alachua Co.	Steadman, 1980
Inglis IA, Citrus Co.	Carr, 1981; Ritchie, 1980; Steadman, 1980
Santa Fe River IIIA, Gilchrist Co.	Steadman, 1980
Williston, Levy Co.	Holman, 1959, 1961; Steadman, 1980
<u>LATE PLEISTOCENE (Rancholabrean)</u>	
Arredondo, Alachua Co.	Brodkorb, 1959; Holman, 1961; Olson, 1974b, 1977b; Steadman, 1976, 1980; Storer, 1976b
Aucilla River IA, Jefferson Co.	Steadman, 1980
Bowman IA, Putnam Co.	Steadman, 1980
Bradenton, Manatee Co.	Becker, 1984; Steadman, 1980; Wetmore, 1931
Catalina Lake, Pinellas Co.	Storer, 1976b
Coleman III, Sumter Co.	Ritchie, 1980
Crystal Spring Run, Pasco Co.	Brodkorb, 1956b
Davis Quarry, Citrus Co.	Steadman, 1980
Econfina River, Taylor Co.	Steadman, 1980
Eichelberger Cave, Marion Co.	Brodkorb, 1955b; Holman, 1961
Florida Lime Company, Marion Co.	Steadman, 1980
Haile IA, Alachua Co.	Brodkorb, 1953a, 1954b; Olson, 1974b, 1977b
Haile IIIA, Alachua Co.	Holman, 1961; Steadman, 1980
Haile VIIA, Alachua Co.	Steadman, 1980

Table 1.1--continued

<u>Locality</u>	<u>Reference (s)</u>
Haile XIB, Alachua Co.	Ligon, 1965; Olson, 1974b
Hog Cave, Sarasota Co.	Steadman, 1980; Wetmore, 1931
Hog Creek, Manatee Co.	Wetmore, 1931
Hornsby Springs, Alachua Co.	Storer, 1976b
Itchtucknee River, Columbia Co.	Campbell, 1980; McCoy, 1963; Olson, 1974a, 1974b, 1977b; Storer, 1976b; Wetmore, 1931
Jenny Spring, Gilchrist Co.	Storer, 1976b
Kendrick IA, Marion Co.	Steadman, 1980
Lake Monroe, Volusia Co.	Holman, 1961; Storer, 1976b
Mefford Cave I, Marion Co.	Steadman, 1980
Melbourne, Brevard Co.	Holman, 1961; Steadman, 1980; Wetmore, 1931
Monkey Jungle, Dade Co.	Ober, 1978
Oakhurst Quarry, Marion Co.	Holman, 1961; Steadman, 1980
Orange Lake, Marion Co.	Holman, 1961
Reddick IB, Marion Co.	Brodkorb, 1952, 1957, 1963e; Hamon, 1964; Holman, 1961; Olson, 1974b, 1977b; Steadman, 1976, 1980; Storer, 1976b
Rock Springs, Orange Co.	Storer, 1976b; Steadman, 1980; Woolfenden, 1959
Sabertooth Cave, Citrus Co.	Holman, 1961; Wetmore, 1931
St. John's Lock, Putnam Co.	Storer, 1976b
St. Mark's River, Leon/Wakulla Co.	Steadman, 1980
Santa Fe River IA, Gilchrist Co.	Steadman, 1980
Santa Fe River IVA, Gilchrist Co.	Steadman, 1980
Seminole Field, Pinellas Co.	Holman, 1961; Olson, 1974b; Steadman, 1980; Wetmore, 1931

Table 1.1--continued

<u>Locality</u>	<u>Reference (s)</u>
Steinhatchee River, Taylor/Dixie Co.	Steadman, 1980
Venice Rocks, Manatee Co.	Wetmore, 1931
Vero (Stratum 2), Indian River Co.	Holman, 1961; Sellards, 1916; Shufeldt, 1917; Steadman, 1980; Storer, 1976b; Weigel, 1962; Wetmore, 1931
Warren's Cave, Alachua Co.	Holman, 1961
Wekiva Run III, Levy Co.	Steadman, 1980
West Palm Beach, Palm Beach Co.	Becker, 1985c
Withlacoochee River, Citrus Co.	Steadman, 1980
Zuber, Marion Co.	Holman, 1961
<u>HOLOCENE</u>	
Cotton Midden, Volusia Co.	Hay, 1902; Neill et al., 1956
Castle Windy Midden, Volusia Co.	Weigel, 1958
Good's Shellpit, Volusia Co.	Steadman, 1980
Green Mound Midden, Volusia Co.	Hamon, 1959
Nichol's Hammock, Dade Co.	Hirschfeld, 1968; Steadman, 1980
Silver Glenn Springs, Lake Co.	Neill et al., 1956; Steadman, 1980
Summer Haven Midden, St. Johns Co.	Brodkorb, 1960
Vero (Stratum 3), Indian River Co.	see Vero, Stratum 2, above
Wacissa River, Jefferson Co.	Steadman, 1980

CHAPTER II
METHODS

Measurements

Measurements made in this study are listed below and are illustrated in Figures 2.1 - 2.4. They have been selected from the literature dealing with the osteology and identification of both Recent and fossil species of birds. Previous authors have dealt with only one specific group (Steadman, 1980; Howard, 1932b; Ono, 1980) or with Recent birds commonly found in archeological sites (von den Driesch, 1979; Gilbert, et al., 1981). The most applicable anatomical studies on fossil birds are by Ballmann (1969a, 1969b). I have modified measurements from the above studies to make them applicable to the range of morphologies encountered in the fossil birds of this study. Measurements for the less diagnostic elements and for the cranium were not included. Measurements presented in the systematic section of this dissertation depend on the fossil material available and the morphology of the species considered.

Anatomical terminology follows Baumel et al. (1979) and Howard (1929, 1980). Many Latin terms have been anglicized for ease of communication, but the original Latin is given parenthetically when the term is first used (below). Terms for soft tissue anatomy come from Feduccia (1975) and Van den Berge (1975).

Scapula

1. LENGTH.--Greatest length from the acromion to the caudal extremity of the scapula (Extremitas caudalis scapulae).
2. W-NECK.--Least width neck of scapula (Collum scapulae).
3. W-PROX.--Proximal width from the ventral tip of the glenoid facet (Facies articularis humeralis) to the dorsal margin of the scapular head (Caput scapulae).
4. ACR-GLN.--Length from tip of acromion through ventral tip of glenoid facet.
5. D-GLN.--Depth of glenoid facet.

Coracoid

1. HEAD-FAC.--Length from head (Processus acrocoracoideus) through external end of sternal facet (Facies articularis sternalis).
2. HEAD-IDA.--Length from head through internal distal angle (Angulus medialis).
3. HEAD-CS.--Length from head through scapular facet (Cotyla scapularis).
4. D-HEAD.--Least depth of head.
5. W-SHAFT.--Width of midshaft.
6. D-SHAFT.--Depth of midshaft.
7. FAC-IDA.--Length from external end of sternal facet through internal distal angle.
8. IDA-PL.--Length from internal distal angle to medial most edge of sternocoracoidal process (Processus lateralis).
9. IDA-PP.--Length from internal distal angle to procoracoid process (Processus procoracoideus).

10. L-GLEN.--Length of glenoid facet from the most cranial portion of glenoid through the most caudal point of scapular facet.
11. IDA-FNS.--Length from internal distal angle through the most sternal edge of coracoidal fenestra (Foramen nervus supracoracoidei).
12. ANG-HEAD.--Angle formed between axis of the head, as seen in proximal view, and the plane parallel to the dorsal surface (Facies dorsalis).

Humerus

1. LENGTH.--Greatest length from the head of the humerus (Caput humeri) through the midpoint of the lateral condyle (Condylus ventralis).
2. W-SHAFT.--Transverse width of midshaft.
3. D-SHAFT.--Depth of midshaft.
4. W-PROX.--Transverse width of proximal end from the external tuberosity (Tuberculum dorsale) to the most ventral face of the bicipital crest (Crista bicipitalis).
5. D-PROX.--Depth of proximal end, from the bicipital surface (Facies bicipitalis) to the internal tuberosity (Tuberculum ventrale), measured at right angles to the long axis of the shaft.
- 5a. D-HEAD.--Depth of head, measured parallel to the axis of the head.
6. L-DELTOID.--Length of deltoid crest (Crista pectoralis), measured from the external tuberosity to the most distal extension of the deltoid crest.

7. W-DIST.--Transverse width of distal end from the entepicondylar prominence (Epicondylus ventralis) to the ectepicondylar prominence (Epicondylus dorsalis).
8. D-DIST.--Depth of distal end from cranial face of external condyle (Condylus dorsalis) through ridge slightly mediad from external tricipital groove (Sulcus scapulotricipitis), measured at right angles to the long axis of the shaft.
9. D-ENTEP.--Depth of entepicondyle (Epicondylus ventralis) from attachment of the pronator brevis (Tuberculum supracondylare ventrale) through entepicondyle (Processus flexoris), measured at right angles to the long axis of the shaft.

Ulna

1. V-LENGTH.--Greatest length from olecranon through tip of internal condyle (Condylus ventralis).
2. W-SHAFT.--Transverse width of midshaft.
3. D-SHAFT.--Depth of midshaft.
4. W-PROX.--Greatest transverse width of proximal articular surface.
5. D-LENGTH.--Length from tip of olecranon to tip of external cotyla (Cotyla dorsalis).
6. D-PROX.--Depth of proximal end from cranial tip of internal cotyla (Cotyla ventralis) to caudal margin (Margo caudalis) of shaft of ulna, measured at right angles to the long axis of the shaft.
7. ECON.--Length from external condyle (Condylus dorsalis) through ventral face of distal end.

8. CPTB.--Length from carpal tuberosity (Tuberculum carpale) through lateral face of distal end.
9. ECON-CPTB.--Length from external condyle through carpal tuberosity.
10. ECON-ICON.--Length from external condyle through internal condyle.

Radius

1. LENGTH.--Greatest length from the radial head (Caput radii) through distal end of the radius (Extremitas distale radii).
2. W-SHAFT.--Transverse width of midshaft.
3. D-SHAFT.--Depth of midshaft.
4. W-PROX.--Greatest transverse width of proximal end.
5. D-PROX.--Greatest depth of proximal end.
6. W-DIST.--Greatest transverse width of distal end.
7. D-DIST.--Greatest depth of distal end.

Carpometacarpus

1. LENGTH.--Greatest length from most proximal portion of the carpal trochlea (Facies articularis radiocarpalis of trochlea carpalis) through facet for digit III (Facies articularis digitalis minor).
 2. W-PROX.--Transverse width proximal end from ligamental attachment of pisiform process (Processus pisiformes) to dorsal surface (Facies dorsalis), measured at right angles to the long axis of the shaft.
- 2a. W-CARPAL.--Transverse width carpal trochlea measured at the proximal edge of the articular facet.

3. D-PROX.--Depth of proximal end from tip of process of metacarpal I (Processus extensoris) through caudal part of carpal trochlea (Facies articularis ulnocarpalis), measured at right angles to the long axis of the shaft.
4. L-MCI.--Length metacarpal I (Os metacarpalis alulare) from process of metacarpal I to pollical facet (Processus alularis).
5. D-SHAFT.--Depth of midshaft of metacarpal II (Os metacarpale majus).
6. W-SHAFT.--Transverse width of midshaft of metacarpal II.
7. D-DIST.--Greatest depth of distal end, measured across dorsal edge of facet for digit II (Facies articularis digitalis major).
8. W-DIST.--Transverse width distal end from edge of facet for digit II through facet for digit III.

Furculum

1. LENGTH.--Greatest length, measured from furcular process to scapular tuberosity.
2. D-PROX.--Greatest diameter of coracoidal facet.

Femur

1. M-LENGTH.--Greatest length from head of femur (Caput femoris) through medial condyle (Condylus medialis).
2. L-LENGTH.--Greatest length from trochanter (Trochanter femoris) through lateral condyle (Condylus lateralis).
3. W-SHAFT.--Transverse width of midshaft.
4. D-SHAFT.--Depth of midshaft.
5. W-PROX.--Transverse width of proximal end, measured from the head of femur through lateral aspect of trochanter, taken at right angles to the long axis of the shaft.

6. D-HEAD.--Greatest depth of femoral head.
7. W-DIST.--Greatest transverse width of distal end.
8. W-M&LCON.--Transverse width of medial and lateral condyles from (Crista tibiofibularis) to medial border of medial condyle.
9. W-LCON.--Transverse width of lateral condyle.
10. W-L&FCON.--Transverse width of lateral condyle and fibular condyle.
11. D-FCON.--Greatest depth of fibular condyle.
12. D-LCON.--Greatest depth of lateral condyle.
13. D-MCON.--Greatest depth of medial condyle.

Tibiotarsus

1. L-LENGTH.--Greatest length from interarticular area (Area interarticularis) on proximal articular surface through lateral condyle (Condylus lateralis).
2. M-LENGTH.--Greatest length from the most proximal portion of cnemial crest (Crista cnemialis cranialis) through medial condyle (Condylus medialis). This includes the patella, if fused, as in loons and grebes.
3. FIBULAR.--Length from interarticular area on proximal articular surface to the most distal point of fibular crest (Crista fibularis).
4. W-SHAFT.--Transverse width of midshaft.
5. D-SHAFT.--Depth of midshaft.
6. W-PROX-M.--Transverse width of proximal articular surface from articular facet for fibular head (Facies articularis fibularis) to medial border of proximal articular surface.

7. D-PROX.--Depth of proximal end from most caudal edge of medial articular face (Facies articularis medialis) to the most cranial point of the cranial cnemial crest.
8. W-PROX-L.--Transverse width of proximal end from medial border of cranial cnemial crest to lateral border of lateral cnemial crest (Crista cnemialis lateralis).
9. W-DIST-CR.--Transverse width of distal end, measured across cranial portion of condyles.
10. W-DIST-CD.--Transverse width of distal end, measured across caudal portion of condyles.
11. D-MCON.--Greatest depth of medial condyle.
12. D-LCON.--Greatest depth of lateral condyle.
13. D-ICON.--Depth of area intercondylaris.

Tarsometatarsus

1. LENGTH.--Greatest length from intercondylar eminence (Eminentia intercondylaris) through trochlea for digit III (Trochlea metatarsi III).
2. W-SHAFT.--Transverse width of midshaft.
3. D-SHAFT.--Depth of midshaft.
4. FLEXOR.--Intercondylar eminence to middle of tubercle for tibialis anterior (Tuberositas m. tibialis cranialis).
5. W-PROX.--Greatest transverse width proximal articular surface, measured across dorsal surface.
6. D-MCOT.--Greatest depth medial cotyla.
7. D-LCOT.--Greatest depth lateral cotyla.

8. D-PROX.--Depth from dorsal edge of proximal articular surface to closest hypotarsal canal (Canalis hypotarsi), or the closest hypotarsal groove (Sulcus hypotarsi), if no canals are present as in the Accipitridae.
9. W-HYPOTS.--Greatest transverse width of hypotarsus.
- 9a. W-HYPOTS-C.--Transverse width of tuberosity on medial hypotarsal crest (Crista medialis hypotarsi), in cormorants only.
10. L-HYPOTS.--Length of medial hypotarsal crest.
11. D-PROX-L.--Depth of proximal end, measured from dorsal edge of the proximal articular surface through the lateral hypotarsal crest (Crista lateralis hypotarsi).
- 11a. D-PROX-M.--Depth of proximal end, measured from dorsal edge of the proximal articular surface through the medial hypotarsal crest, if the lateral hypotarsal crest is reduced.
12. L-MTI.--Greatest length of metatarsal I facet (Fossa metatarsi I).
13. D-D-SHAFT.--Depth of shaft at cranial edge of distal canal (Foramen vasculare distale).
14. W-DIST.--Greatest transverse width of distal end (if trochlea are of equal length).
15. TRIII-TRIV.--Greatest transverse width from trochlea III through trochlea IV (if trochlea II is elevated).
16. TRII-TRIV.--Greatest transverse width between plantar portion of trochlea II and plantar portion of trochlea IV.
17. W-TRII.--Greatest transverse width of trochlea II.
18. D-TRII.--Greatest depth of trochlea II.
19. W-TRIII.--Greatest transverse width of trochlea III.

20. D-TRIII.--Greatest depth of trochlea III.
21. W-TRIV.--Greatest transverse width of trochlea IV.
22. D-TRIV.--Greatest depth of trochlea IV.

Computer Software

Biomedical Statistical Software, P-Series (Dixon, 1981) was used to analyze many of the measurements. Programs used included BMDP1D (simple descriptive statistics), BMDP6D (bivariate plots), and BMDP2M (cluster analysis). Computations were made at the Northeast Regional Data Center (NERDC) at the University of Florida, Gainesville.

Nomenclature

Common names have not been used for species. Few nomenclatural systems have a more unstable, inaccurate, or confusing set of terms than the American Ornithologists' Union's (1983) list of common names for birds. I agree with J. L. Peters (1934:ii)

. . . inventing common English names for birds that do not have them is a waste of time. After all, the primary reason for a scientific name is to have a name intelligible to scientists the world over.

Systematic nomenclature generally follows the Checklist of Birds of the World (Mayr and Cottrell, 1979; Peters, 1931-1951) for Recent species and Brodkorb's Catalogue of Fossil Birds (1963-1978) for fossil species. Departures are accompanied by full citation.

Figure 2.1. Schematic diagrams illustrating measurements of the humerus, coracoid, and scapula. A. Humerus, cranial view. B. Humerus, ventral view. C. Coracoid, dorsal view. D. Coracoid, lateral view. E. Humerus, distal end view. F. Scapula, lateral view. G. Scapula, proximal end view. Figures are not drawn to scale. Measurements defined in the text.

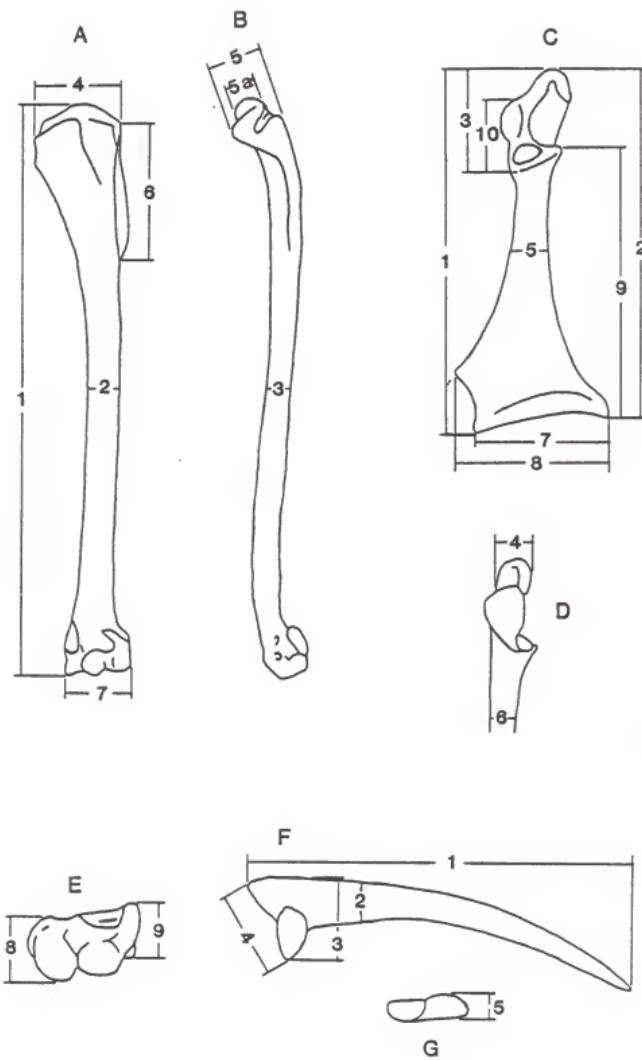


Figure 2.2. Schematic diagrams illustrating measurements of the radius, ulna, carpometacarpus, and furculum. A. Radius, medial view. B. Radius, cranial view. C. Ulna, cranial view. D. Ulna, caudal view. E. Carpometacarpus, ventral view. F. Carpometacarpus, proximal end view. G. Carpometacarpus, distal end view. H. Ulna, distal end view. I. Furculum, lateral view. Figures are not drawn to scale. Measurements are defined in text.

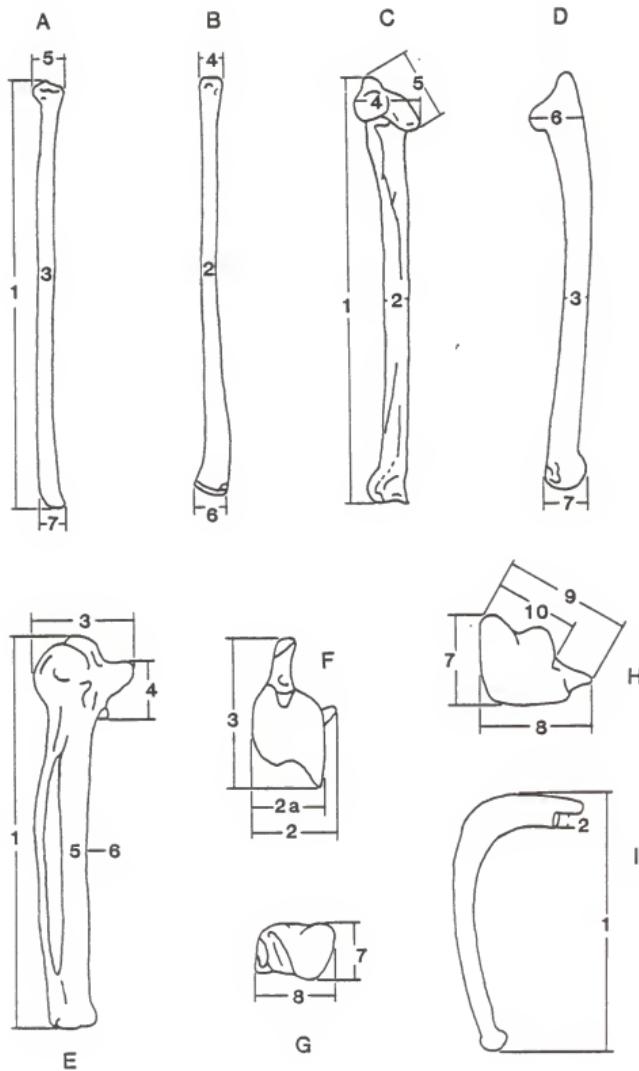


Figure 2.3. Schematic diagrams illustrating measurements of the femur and tibiotarsus. A. Tibiotarsus, caudal view. B. Tibiotarsus, proximal end view. C. Tibiotarsus, distal end view. D. Femur, cranial view. E. Femur, proximal end view. F. Femur, distal end view. G. Femur, caudal view of distal end. Figures are not drawn to scale. Measurements are defined in the text.

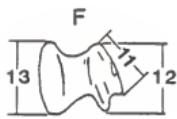
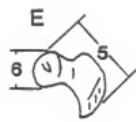
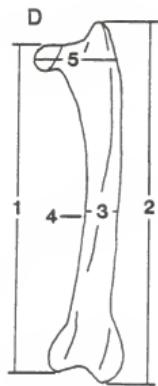
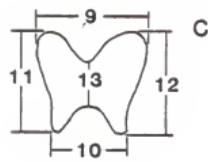
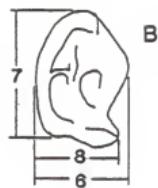
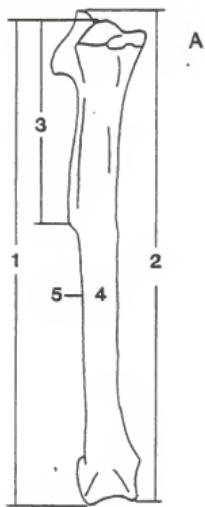
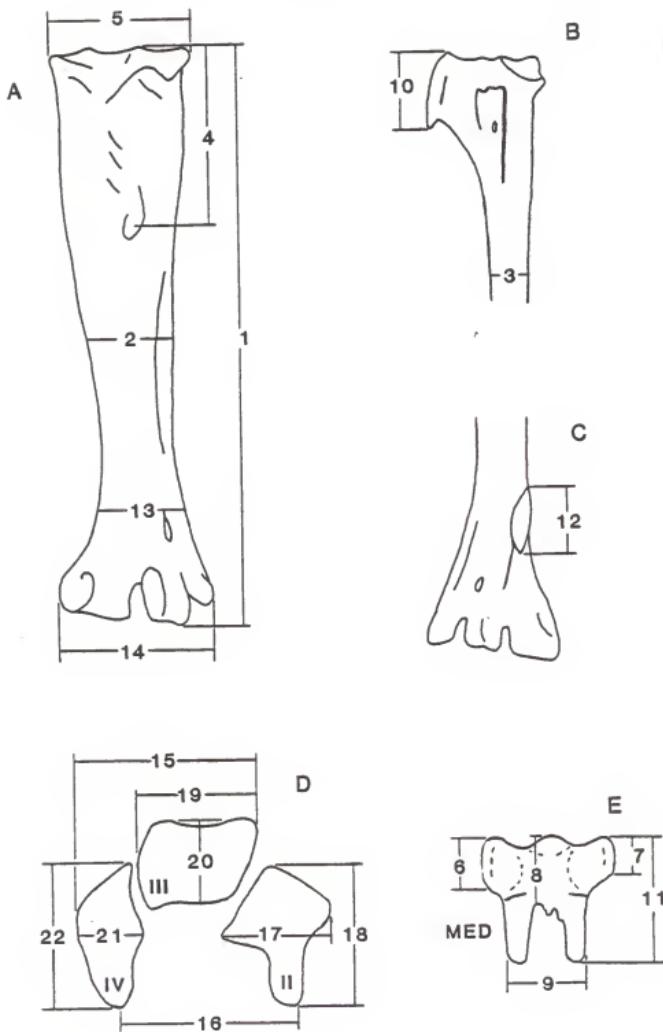


Figure 2.4. Schematic diagrams illustrating the measurements of the tarsometatarsus. A. Dorsal view. B. Lateral view. C. Plantar view of distal end. D. Distal end view. E. Proximal end view. Figures are not drawn to scale. Measurements are defined in text.



Systematics

I have associated the skeletal elements of the fossil taxa in this study using the following general criteria (Howard, 1932b):

1. resemblance to other species.
2. size and proportion.
3. relative abundance.

Systematic reasoning and taxonomic practice generally follow Mayr (1981), when possible. Skeletal elements are first grouped into similarity classes by means of measurements and qualitative characters. Each identifiable taxon is placed within a genealogy of previously known species by the hierachial distribution of shared-derived characters, and the new species are then integrated into an evolutionary classification.

Paleoecology

Paleoecological methods are described by Shipman (1981). See the paleoecology section for further comments on the paleoecological methods used in the excavation of the localities included in this study.

Biochronology and Faunal Dynamics

A database for the examination of the biochronology and the faunal dynamics of fossil birds of the Neogene of North America was developed from the following sources: (1) A literature survey of all fossil localities in North America from the late Arikareean through the Blancan that have produced fossil birds. This published information was then emended to reflect the current concepts of geological formations, geological correlations, mammalian systematics, and the relative and absolute dating of fossil localities. Verification of all fossil identifications was made whenever possible. (2) Information from other

major unpublished localities was added to this database. This produced a total of 133 localities from the Neogene of North America (86 published, 47 unpublished) with a record of fossil birds. (3) The occurrences of fossil taxa were condensed to tabular form to reflect the actual, documented range of taxa at the family, subfamily, and generic level. A given taxonomic range reflects the summation of all lower taxonomic ranks plus material which is only diagnostic to that given level. (4) From this table, geological ranges were inferred parsimoniously. For example, if a genus is known from the early Hemingfordian and the late Clarendonian, I inferred that it also occurred in North America during the interval between these endpoints. (5) From this table (#3 above), biochronologically useful species were identified.

Indices of avian faunal dynamics were calculated following Marshall et al. (1982): the duration (*d*) of each land mammal age is given in millions of years, to the nearest tenth, and is based on all available data; diversity (*Si*) represents the total number of genera known for each land mammal age; originations (*Oi*) are the number of generic first appearances in a given land mammal age; extinctions (*Ei*) are last appearances of a genus in a given land mammal age; running means (*Rm*) compensates for time intervals of unequal duration by subtracting the average of originations (*Oi*) and extinctions (*Ei*) for a given age from the diversity (*Si*) of that age, or $Rm = Si - (Oi + Ei)/2$; origination rates (*Or*) adjust for unequal time intervals by dividing the total number of generic originations (*Oi*) occurring during a given land mammal age by the duration (*d*) of that interval; similarly, the extinction rate, $Er = Ei/d$; turnover rates (*T*) are the average number of genera that either originate or go extinct during a given land mammal age, or $T = (Or +$

$Er)/2$; per-genus turnover rate is the turnover rate adjusted for average diversity, calculated by dividing the total turnover rate (T) by the total running mean (Rm). A sampling index was calculated as the number of localities per Land Mammal Age divided by the duration of that interval. Marshall et al. (1982) should be referenced for additional qualifications of each statistic.

Specimens Examined

Fossil specimens included in this study are housed in the collections of the Florida State Museum (UF), the collection of Pierce Brodkorb (PB), and the Frick collections of the American Museum of Natural History (F:AM). I have tried to include all known avian material from the late Miocene through early Pliocene from Florida within these collections. Non-diagnostic skeletal elements (vertebrae, phalanges, etc.) were not considered. Fossil material accessioned into the UF collections after 01 June 1984 (primarily from Bone Valley) was not included in this study.

I relied on Recent comparative material in the collections of P. Brodkorb, Florida State Museum, United States National Museum, American Museum of Natural History, University of Michigan, and Royal Ontario Museum.

Abbreviations

Table 2.1 lists the common abbreviations and acronyms used in this dissertation. Anatomical abbreviations were given earlier.

Table 2.1. List of acronyms of institutions and abbreviations of terms used in the text.

<u>Acronym</u>	<u>Institutions/Collections</u>
AMNH	American Museum of Natural History
F:AM	Frick Collections, American Museum of Natural History
LACM	Los Angeles County Museum of Natural History
MCZ	Museum of Comparative Zoology, Harvard University
PB	Collection of Pierce Brodkorb
ROM	Royal Ontario Museum
UF	Florida State Museum, University of Florida
UM	University of Michigan
UMCP	University of California, Museum of Paleontology, Berkeley
UNSM	University of Nebraska State Museum
USNM	United States National Museum
YPM	Yale Peabody Museum

<u>Abbreviation</u>	<u>Terms</u>
BMDP	Biomedical Statistical Program, P-series
l. f.	local fauna
M.	<i>musculus</i>
MA	megannum (or million years)
max.	maximum
min.	minimum
mm.	millimeter
MYBP	million years before present
N	number (of specimens)
NALMA	North American Land Mammal Age

CHAPTER III GEOLOGY

Biochronology

The Clarendonian and Hemphillian land mammal ages were first proposed by Wood et al. (1941) based on the stage of evolution of mammals from two localities in the panhandle of Texas. Since then, the concept of each has changed, owing to the increasing knowledge of this time period in North America. Two additional ages were proposed by Schultz et al. (1970) for parts of the time intervals covered by the original definitions: the Valentinian (for the late Barstovian to early Clarendonian) and the Kimballian (originally proposed as late Hemphillian; now considered to be early Hemphillian). Neither has been accepted for use on a continent-wide basis. Rather, each has been applied only to fossils from the type formations of the proposed ages (Valentine and Kimball formations). Pertinent references include Schultz et al. (1970), Tedford (1970), Tedford et al. (in press), Breyer (1981), and Voorhies (1984).

The Clarendonian, in the restricted sense of Tedford et al. (in press) is defined on the

earliest appearance of Barbourofelis and, later in the interval, Platybelodon, Amebelodon, and Ischyriictis (Hoplictis). Characterization - earliest appearance of Nimravides, Epicyon (in the Great Plains and Gulf Coast), Griphippus [=Pseudhipparion], Astrohippus, Nannippus (Gulf Coast), Macrogenys, Synthetoceras, Hemiauchenia, Megatylopus, Antilocaprinae (Plioceras and Proantilocapra), latest occurrence of Eucastor, Brachypsalis, Ischyrocyon, Cynarctus, Aelurodon, Tomarctus, Hypohippus, Megahippus, Merychippus, Paratoceras, Miolabis, Protolabis, and probably Ustatochoerus.

In Florida, common late Clarendonian taxa include Barbourofelis, Nimravides, Mylagaulus, Pseudhipparion, Amebelodon, advanced species of Eucastor, Pediomeryx, and Aelurodon.

The early Hemphillian is defined (Tedford et al., in press) by the earliest appearance of Arvicolinae (limited occurrence of Microtoscopes and Paramicrotoscopes), Pliotomodon, and Megalonychidae (Pliometanastes), limited occurrence late in interval of Simocyon, Indarctos, Plionarctos, Lutravus, and Eomellivora, and earliest appearance, late in interval, of Mylodontidae (Thinobadistes), Machairodus and the Bovidae (Nectragocerus). Characterization - earliest appearance of Dipoides, Pliosaccomys, Pliotaxidea, Vulpes, 'Canis', Osteoborus, and Cranioceras (Yumaceras), latest occurrence of Amphicyonidae, Leptarcetus, Sthenictis, Nimravides, Barbourofelis, Epicyon, Plichippus, Protohippus, Cormohipparion, Prosthenops, Aepycamelus, Pseudoceras and Plioceras.

In Florida, common early Hemphillian taxa include Calippus, Pediomeryx (Yumaceras), Aepycamelus, primitive species of Osteoborus, Cormohipparion, and Nannippus, and advanced species of Epicyon. The early sloths Pliometanastes and Thinobadistes are present. The Eurasiatic immigrants Indarctos and Machairodus appear in the later part of the early Hemphillian.

The late Hemphillian is defined (Tedford et al., in press) by the limited occurrence of Promimomys, 'Propliophenacomys', Plesiogulo, Agriotherium, and Plionarctos and the earliest appearance of Megalonyx, Ochotona, Megantereon, Felis, Enhydriodon, and Cervidae. Characterization - earliest appearance of Taxidea, Borophagus, Rhynchotherium, Platygonus, and Mylohyus, limited occurrence of Pediomeryx, latest occurrence of Mylagaulidae, Osteoborus, Astrohippus, Neohipparion, Dinohippus and Rhinocerotidae.

In Florida, common late Hemphillian taxa include advanced species of Osteoborus, Neohipparion, Nannippus, Pseudhipparion, Teleoceras, and Hipparion. Also present are Plesiogulo, Megalonyx, antilocaprids, Agriotherium, Enhydriodon s.l., Megantereon, Machairodus, Rhynchotherium, Pliomastodon, Dinohippus, Plionarctos, Felis, and cervids.

Local FaunasLove Bone Bed

The Love Bone Bed is located near the town of Archer, Alachua County, along State Road 241, in the NW 1/4, SW 1/4, NW 1/4, Sec. 9, T. 11 S., R. 18 E., Archer Quadrangle, U. S. Geologic Survey 7.5 minute series topographical map, 1969. Excavation and collection of fossil vertebrates by the Florida State Museum took place from its discovery in 1974 until the quarry was closed during the summer of 1981. This local fauna originated from the Alachua Formation (Williams et al., 1977).

The Love Bone Bed is considered latest Clarendonian in age (Webb et al., 1981). Studies published to date on the Love Bone Bed and its vertebrate fauna include a general overview of the geology and paleontology of the locality, including a preliminary faunal list (Webb et al., 1981); studies on the turtles Pseudemys caelata, and Deirochelys carri (Jackson, 1976, 1978); a description of the rodent Mylagaulus elassos Baskin (1980); description of the carnivores Barbourofelis lovei and Nimravides galiani Baskin (1981); descriptions of the procyonids Arctonasua floridana and Paranasua biradica Baskin (1982); the description of the ruminant Pediomeryx hamiltoni Webb (1983); and a population study on the three-toed horse Neohipparrison cf. N. leptode (Hulbert, 1982). Studies on fossil birds include papers on the fossil herons (Becker, 1985a), a description of a new species of osprey (Becker, 1985b), and one on the fossil anhinga (Becker, ms.). Additional studies are in progress.

Mixson Bone Bed

The Mixson Bone Bed is located approximately 2 miles northeast of Williston, Levy County, in the NE 1/4, SW 1/4, Sec. 29, T. 12 S., R. 19 E., Williston Quadrangle, U. S. Geological Survey 7.5 minute series topographical map, 1969. This is the type locality of the Alachua Formation (Dall and Harris, 1892). There have been many studies on this site, including papers by Leidy and Lucas (1896), Sellards (1916), Hay (1923), Simpson (1930), Webb (1964, 1969, in press), and Harrison and Manning (1983). Additional references are listed in Ray (1957).

Genera in common with McGehee include Calippus, Pediomeryx (Yumaceras), Aepycamelus, Osteoborus, and Aelurodon (Webb, 1969). The early Hemphillian mylodontid sloth Thinobadistes is present. Two other early Hemphillian index genera are absent from this local fauna, although they are present in other Florida sites--Pliometanastes, and Indarctos. The first appearance of Indarctos occurs late in the early Hemphillian and its absence in this local fauna probably has temporal significance. The absence of Pliometanastes is usually considered an ecological sampling bias.

McGehee Farm

This locality is almost exactly three miles north of Newberry, Alachua County, along State Highway 45, S1/2, NW1/4, Sec. 22, T. 9 S., R. 17 E., Newberry Quadrangle, U. S. Geologic Survey 7.5 series topographical map, 1968, in northcentral Florida. This locality was first discovered in 1958 and was extensively collected by the University of Florida, with support of the Frick Corporation. This local fauna originates from the Alachua Formation, and the geology of this locality is briefly discussed by Webb (1964) and Hirschfeld and Webb (1968). The

latter publication includes a preliminary list of the fossil vertebrates from this local fauna. No faunal revision of this locality has been undertaken, but several papers treating specific groups have appeared (sloths: Hirschfeld and Webb, 1968; mylagaulids: Webb, 1966; canids: Webb, 1969; and protoceratids: Patton and Taylor, 1973).

The faunal composition of this local fauna indicates an early Hemphillian age (Hirschfeld and Webb, 1968; Webb, 1969; Marshall et al., 1979), based primarily on the presence of Pliometanastes, the early Hemphillian megalonychid ground sloth. Typical early Hemphillian mammalian genera present include Calippus, Pediomeryx (Yumaceras), Aepycamelus, Osteoborus, and Aelurodon (Webb, 1969).

The birds of this locality were first studied by Brodkorb (1963a) who reported Phalacrocorax wetmorei, and described two new species-- Nycticorax fidens and Ereunetus rayi. Later, Olson (1976) described Jacana farrandi from here.

Withlacoochee River 4A

The Withlacoochee River 4A local fauna lies approximately 8 km. southeast of Dunnellon (center of N1/2, NW1/4, Sec. 30, T. 17 S., R. 20 E., Stokes Ferry Quadrangle, U. S. Geologic Survey 7.5 minute series topographical map, 1954, Marion County), in northcentral Florida. The fossil vertebrates originate from a massive green clay filling of a sinkhole in the late Eocene Inglis Formation of the Ocala Group (Webb, 1969, 1973, 1976). This deposit of green clay is being eroded by the Withlacoochee River; the fossils were collected in approximately 20 feet of water using scuba equipment. Deposition almost certainly occurred in a pond environment near sea-level as shown by the fine-grained sediments

with articulated fish skeletons, the present elevation, and the marine taxa present (Becker, 1985a; Berta and Morgan, in press).

Studies on the fossil mammals from here include Webb's (1969) paper on Osteoborus orc, Hirschfeld and Webb's (1968) study on Pliometanastes protistus, Webb's (1973) mention of antilocaprids, and Wolff's (1978) study of the cranial anatomy of Indarctos. The concurrent range zones of the first two taxa, and the presence of Indarctos, Machairodus, and Pseudoceras indicate an age of late early Hemphillian.

Fossil birds from here include a very small species of Egretta and an indeterminate species of Buteo (Becker, 1985a). A preliminary faunal list is included in this paper.

Haile VB

This locality is from the NE 1/4, Sec. 23, T. 9 S., R. 18 E., Newberry Quadrangle, U. S. Geologic Survey 7.5 minute series topographical map, 1968. Auffenberg (1954) discusses the geology of this locality and describes the abundant material of Gavialisuchus americanus (Sellards) from this locality. A number of equids are known from this site including Pliohippus, Cormohipparion, Calippus, and Nannippus.

Haile VI

This locality is in the N1/2, SW1/4, Sec. 24, T. 9 S., R. 17 E., Newberry Quadrangle, U. S. Geologic Survey 7.5 minute series topographical map, 1968, Alachua County, Florida. It was collected by the Florida Geologic Survey and Florida State Museum. Auffenberg (1963) discussed the geology and concluded that this locality represents a stream deposit. The mammalian fauna includes 'Hipparion', Pseudoceras, and the type of Mylagaulus kinseyi Webb (1966). A new species of

sparrow, Palaeostruthus eurius, was described from here (Brodkorb, 1963a). Reptiles known from here include Deirochelys and Gavialosuchus.

Haile XIXA

This locality is 2.5 miles NE of Newberry, Alachua County, in the NE 1/4, Sec. 26, T. 9 S., R. 17 E., Newberry Quadrangle, U. S. Geologic Survey 7.5 minute series topographical map, 1968. It was collected by the Florida State Museum staff. Vertebrates are mainly aquatic, including a large amount of skeletal material of Gavialosuchus. Fossil mammals present include Epicyon, geococids, Pediomeryx, equids, and Aepycamelus.

Bone Valley Mining District

The name "Bone Valley" is applied to the phosphate mining district of central Florida, mainly in Polk County, but also including portions of adjacent Hillsborough, Hardee, and Manatee counties. The vertebrate fauna was first described by Sellards (1916) and later more fully studied by Simpson (1930). Berta and Morgan (in press) present an account of the present status of vertebrate paleontology of this area. Much of the following comes from their paper.

Most of the fossil vertebrates from the Bone Valley area were obtained from extensive open-pit phosphate mines. In situ collections are rare and make up approximately 5 - 10 % of the Florida State Museum collections, part of the USGS and USNM collections, and virtually none of the Harvard collections. Avian fossils from these in situ sites are very rare. Fossils are more commonly found eroding from spoil piles after an area has been strip-mined. Except for the in situ collections and a few intensively collected concentrations, the fossil vertebrates collected

from one mine, or a single dragline operating within one mine, are considered as coming from one broad "locality." The exact geographic position of these localities range from precisely known (1/4, 1/4, 1/4 section) to generally known (from one mine--i.e. somewhere within 1 to 10 sections). For a few amateur collections where even the mine is unknown, the only designation can be the Bone Valley Mining District (i.e. somewhere within 100 square miles), but the majority of specimens are identified as coming from one mine. Table 3.1 lists the mines, mine codes, describes their approximate location, and lists the stratigraphic codes used.

The age of the Bone Valley fossil vertebrates was much debated from the 1920s through the 1950s (discussed in Brodkorb 1955a), with the proposed age ranging from the Miocene through the Pleistocene. Brodkorb (1955a), using a Lyellian method of percent extinct species in the fauna and the temporal ranges of three species, suggested that the age of the Bone Valley avifauna was between the late Miocene and middle Pliocene, probably early or middle Pliocene (i.e. Clarendonian or Hemphillian; = late Miocene of current usage).

The majority of fossil land mammals are late Hemphillian in age and compare well with others of similar age in North America. There is no evidence to suggest that the fossil birds, which are found in association with these land mammals, are of a different age. Recently several older local faunas (Barstovian, Clarendonian, and early Hemphillian) have been found (MacFadden, 1982; MacFadden and Webb, 1982; Webb and Crissinger, 1984; Berta and Galiano, 1984; and Tedford et al., in press). These older occurrences are from the Phosphoria, Nichols, Silver City, and Kingsford mines and to my knowledge have produced no fossil birds. There

are also numerous Pleistocene sites in the Payne Creek Mine (Steadman, 1984), Peace River Mine (=Pool Branch; Webb, 1974), and Nichols Mine. The Pleistocene fossil birds from these sites can usually be separated from geologically older specimens by their association with Pleistocene fossil land mammals. The Pleistocene fossil birds are not considered in this study.

There have been many recent studies on non-marine mammalian taxa from Bone Valley (Baskin, 1982; Berta and Galiano, 1983; Berta and Morgan, in press; Harrison, 1981; MacFadden and Waldrop, 1980; MacFadden and Galiano, 1981; MacFadden, 1984; Webb, 1969, 1973, 1983; Webb and Crissinger, 1984; Wright and Webb, 1984), but no single faunal study of terrestrial mammals from this local fauna. Reference to the earlier papers published on the Bone Valley Mining District and its vertebrate fauna are given by Ray (1957).

Bone Valley taxa which are typical of the late Hemphillian age include the Eurasian immigrant taxa Agriotherium, Plesiogulo, 'Enhydriodon', and Cervidae. Other taxa present are Rhynchotherium, Hexameryx, and advanced species of Osteoborus, Gomphotherium, Pseudhipparion, Nannippus, and Dinohippus (Berta and Morgan, in press). Other authors (MacFadden and Galiano, 1981; Berta and Galiano, 1983; Wright and Webb, 1984) suggest that the upper Bone Valley Formation is very late Hemphillian because of the presence of taxa equally indicative of an early Blancan age such as Felis rexroadensis, Meganteron hesperus, Dinohippus mexicanus, Mylohyus elmorei, Antilocapra (Subantilocapra), Hemiauchenia, Nasua, and Platygonus.

The birds from Bone Valley have been studied by Brodkorb (1953b, 1953c, 1953d, 1953e, 1955a, 1970). His monograph (1955a) dealt with the

birds then known, primarily the more numerous marine birds. Table 3.2 gives a partial list of birds now known from the Bone Valley Mining District and notes the taxa (marine) not included here. The majority of birds here studied have been collected in the last 15 years and mainly include the rarer, non-marine members of this avifauna.

Manatee County Dam Site

This local fauna originates from a borrow pit south of the Manatee River in Sec. 30, T. 3 $\frac{1}{4}$ S., R. 20 E., Verna Quadrangle, U. S. Geologic Survey 7.5 minute series topographical map, 1944, Manatee County. Like the nearby SR-64 local fauna discussed below, the Manatee County Dam Site is essentially an outlier of the classic Bone Valley local fauna. All three share a similar fauna, geology, and paleoecology. Webb and Tessman (1968) describe this local fauna and report the presence of one bird, Phalacrocorax wetmorei.

SR-64

This locality is located 6 miles east of I-75 along State Road 64 in Sec. 35, T. 3 $\frac{1}{4}$ S., R. 19 E., Manatee County, Lorraine Quadrangle, U. S. Geological Survey 7.5 minute series topographical map, 1973, Florida. It was discovered by Philip Whisler, of Venice, Florida, in 1983. The majority of fossil vertebrates are in his private collection, except for a few specimens in the Florida State Museum collections. Numerous fossil vertebrates are recorded from here, including several species of bony fish, sharks, rays, and several different turtles. Mammals include odobenids, phocids, Schizodelphis, Megalodelphis, tremarctine ursids, cf. Agriotherium, felids, Nannippus minor, Neohipparrison eurystyle, Rhinocerotids, and Hexameryx. Based on the presence of Nannippus minor,

Neohippurion eurystyle, and Hexameryx, this locality is late Hemphillian in age. As for the Manatee County Dam Site, this locality is here considered an outlier of the classic Bone Valley Formation.

Eustatic Sea-Level Changes

Webb and others (Webb and Tessmann, 1968; MacFadden and Webb, 1982; Webb, 1984) have proposed a model using the present elevations of fossil localities with marine or estuarine taxa to reflect the fluctuations of sea-levels during the late Miocene and early Pliocene in peninsular Florida. This scheme is predicated on two assumptions--that the Florida peninsula had been tectonically stable over the later Cenozoic and that the sedimentary sequence reflects actual sea-level change. If these assumptions are valid, then the present elevation of the localities which contain marine or estuarine taxa should reflect the elevation of the ocean at the time when these localities were deposited.

The following evidence argues against this model: (1) The relict Pleistocene shorelines increase in elevation from a low point in southern Georgia to a maximum elevation in northern peninsular Florida and gradually lose elevation to the south. This indicates that the northern part of peninsular Florida has not been stable, and has been differentially uplifted. Opdyke et al. (1984) argue that this occurred during the Pleistocene due to the subsurface solution of limestone and the concomitant isostatic uplift and document an uplift in the magnitude of 30-50 meters since this time. Most of the high-sea-level localities are from the northern part of Florida in highly karsted areas. (2) The elevational changes between most localities could easily be accounted for by a slight regional dip to the beds. For example, a dip of 1/20 of 1 degree would account for an elevational difference of 138

feet over 30 miles (the distance between the Manatee County Dam Site and the "classic" Bone Valley exposures). This would also account for the mixture of land and marine vertebrates in these sites, presuming the tilting is post-depositional.

There is no question that there were eustatic sea-level changes during this time period, such as the Messinian. But the elevations of the Florida fossil vertebrate localities are of very doubtful value as evidence. It should be noted that the rejection of the above hypothesis does not prevent using the faunal composition of these localities to determine their relative proximity to the ocean at the time of deposition. They simply cannot be used as an absolute scale to measure vertical sea-level changes.

Figure 3.1. Correlation Chart of Included Local Faunas.

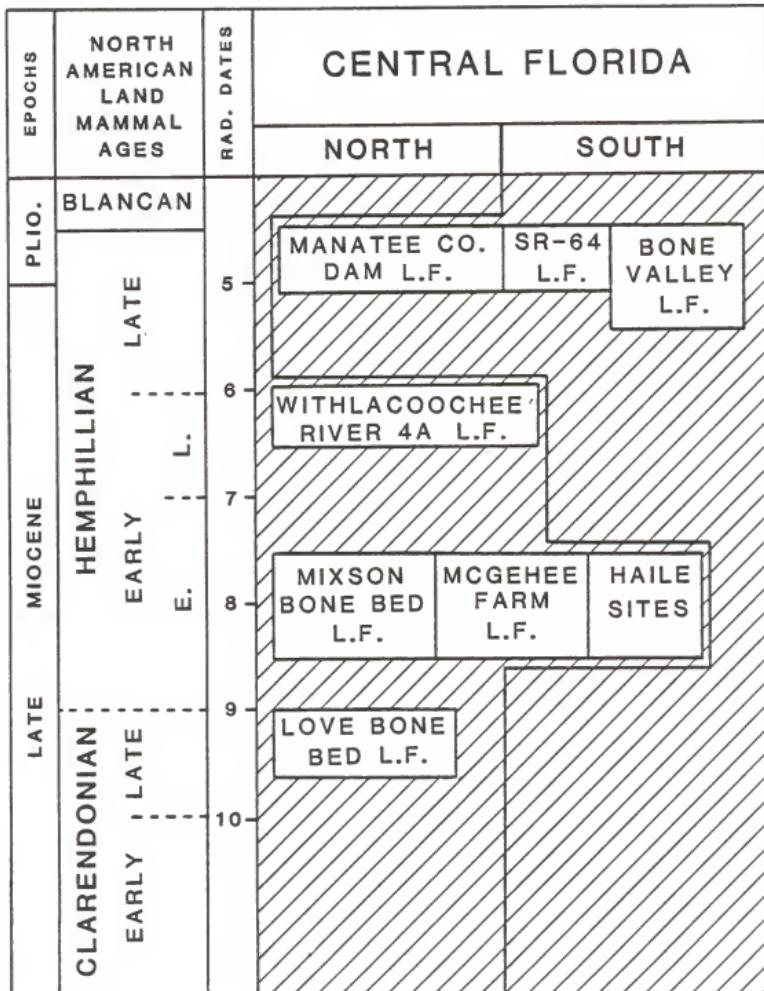


Figure 3.2. Location of Included Local Faunas.

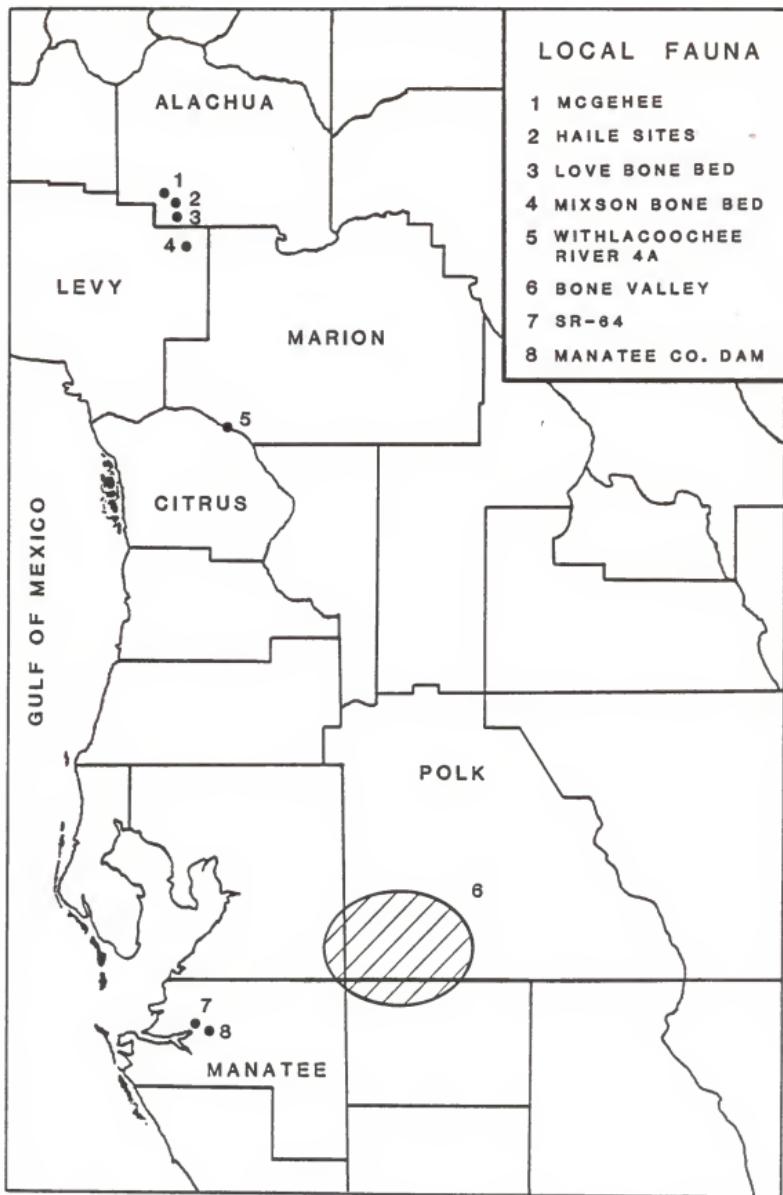


Table 3.1. A partial list of Bone Valley mines, their mine codes, approximate location, and the stratigraphic codes commonly used.

<u>Mines</u>	<u>Codes</u>	<u>Township</u>	<u>Range</u>	<u>Sections</u>
Chicora	BVC			
District Grade	BVPC	see Payne Creek Below		
Estech	BVS	see Swift Below		
Ft. Green	BVFG	32S	23E	2,3,10-14,22-24
Ft. Meade	BVFM	31S	25E	2,13
Gardinier	BVG	32S	24,24E	unknown
Hooker's Prairie	BVHP	31S	24E	17,18,20,28-30
Kingsford	BVK	31S	23E	3
New Palmetto	BVNP	32S	24E	3
Nichols	BVN	30S	23E	19,28,29
Palmetto	BVP	32S	24E	9,10,15,16,21,22
Payne Creek	BVPC	32S	24E	13,14,23,24,29-32
Peace River	BVFM	see Ft. Meade Above		
Swift	BVS	31S	24E	14
Tiger Bay	BVTB	31S	24E	12

<u>Stratigraphic Codes</u>	<u>Explanation</u>
0	No stratigraphic data
1	In place Hawthorn Fm. -- dolomitic
2	In place "lower Bone Valley Fm."
3	In place "upper Bone Valley Fm."
4	In place Pleistocene sediments
5	Soil zone (upper clay)

Table 3.2 Checklist of birds from the late Miocene and early Pliocene Bone Valley Mining District. Asterisks denote marine taxa, which are not included in this study. Taxa are based on previously published works and on original identifications.

*Family Gaviidae	Family Ciconiidae
<u>Gavia palaeodytes</u>	<u>Ciconia</u> sp.
<u>Gavia concinna</u>	Family Anatidae
Family Podicipedidae	<u>Bucephala ossivallalis</u>
<u>Podiceps</u> sp.	Family Pandionidae
<u>Pliodutes lanquisti</u>	<u>Pandion</u> sp.
*Family Diomedidae	Family Accipitridae
<u>Diomedea anglica</u>	<u>Haliaeetus</u> sp.
Family Phalacrocoracidae	<u>Buteo</u> sp.
<u>Phalacrocorax wetmorei</u>	Family Scolopacidae
<u>Phalacrocorax idahensis</u>	<u>Calidris pacis</u>
*Family Sulidae	<u>Erolia penpusilla</u>
<u>Morus peninsularis</u>	<u>Limosa ossivallalis</u>
<u>Sula guano</u>	Family Phoenicopteridae
<u>Sula phosphata</u>	<u>Phoenicopterus floridanus</u>
*Family Procellariidae	*Family Haematopidae
*Family Pelecanidae	<u>Haematopus sulcatus</u>
<u>Pelecanus</u> sp.	*Family Laridae
Family Plataleidae	<u>Larus elmorei</u>
<u>Eudocimus</u> sp.	*Family Alcidae
Family Ardeidae	<u>Australca grandis</u>
<u>Ardea polkensis</u>	

CHAPTER IV
SYSTEMATIC PALEONTOLOGY

Table 4.1 lists the non-marine avian taxa now known to occur in Florida during the late Miocene and early Pliocene. In the following systematic section, I have tried to present osteological characters which define the taxonomic groups in a hierarchical fashion. However, considering the relatively small number of fossil and recent specimens available for some species, and the restricted geographical area from which many of the Recent species were collected, I would not be surprised if some "diagnostic" characters do not hold when a larger number of specimens are examined.

Order Podicipediformes (Fürbringer, 1888)

Family Podicipedidae (Bonaparte, 1831)

Tribe Podilymbini Storer, 1963

Characters. Separate canal through hypotarsus for the tendon of insertion of *M. flexor perforatus digitii II* (Storer, 1963). Murray (1967) gives additional osteological characters for the separation of the different taxa of this family.

Genus Rollandia Bonaparte, 1856

Rollandia sp.

Material. Love Bone Bed local fauna, questionably referred; UF 29670, UF 29673, right coracoids; UF 25815, left coracoid.

Mixson Bone Bed local fauna; F:AM FLA-120-2183, complete right tarsometatarsus.

McGehee Farm local fauna; UF 9488, shaft and distal end of right humerus; UF 12468, right coracoid.

Description. Humerus (UF 9488) poorly preserved; larger and much more robust than both species of Tachybaptus (dominiclus and ruficollis). Morphology of distal end similar to that of Rollandia rolland, but shaft more robust. Measurements given in Table 4.2.

Coracoids from the Love Bone Bed are extremely worn and are here assigned strictly on the basis of their size being near Rollandia (larger than all species of Tachybaptus and smaller than the smallest males of Podilymbus podiceps). Shaft similar to, or slightly more robust than, that of Rollandia rolland. Proximal edge of ventral sternal articulation flared (as in Rollandia rolland, less so in Tachybaptus). Coracoid from McGehee Farm local fauna (UF 12468) similar to those from the Love Bone Bed, except by having a proportionally longer shaft. Measurements are given in Table 4.2.

Overall length of tarsometatarsus similar to Rollandia rolland chilensis. Distinguished from Podilymbus by lacking the cranial expansion of the proximal end of the tarsometatarsus and by having trochlea II placed lower on the shaft. Distinguished from Podiceps species by having the shaft less laterally compressed. Tarsometatarsus differs from that of Rollandia rolland chilensis by having a more deeply excavated lateral parahypotarsal fossa, a hypotarsus with a smaller transverse width, a more distinct ridge extending distally from the hypotarsus, and trochlea II slightly more narrow. Measurements given in Table 4.3.

Remarks. This species appears to be slightly more robust than the modern Rollandia rolland chilensis. The lack of a series of modern sexed

skeletons, necessary to determine the variability of the characters used above, prevents the naming of this species as new.

Genus Tachybaptus Reichenbach, 1853

Tachybaptus sp. indet.

Material. Love Bone Bed local fauna; UF 25796, UF 25817, UF 25818, UF 29671, complete left coracoids; UF 29668, UF 29669, UF 29672, humeral ends left coracoids; UF 26006, UF 26014, UF 26017, UF 26019, UF 29664, UF 29665, UF 29666, UF 29669, complete right coracoids. UF 25773, complete right femur. UF 29663, proximal end of right tibiotarsus (questionably referred).

McGehee Farm local fauna; UF 67810, proximal end right tibiotarsus (questionably referred).

Description. All coracoids are waterworn, abraded, or broken to varying degrees, making detailed descriptions difficult. All coracoids near that of Tachybaptus dominicus in size and overall shape. Additional description is not possible.

Femur also near Tachybaptus dominicus in size and general morphology, but the femoral shaft slightly more gracile. Depression cranial to the patellar sulcus is absent in fossil. Measurements are given in Table 4.4.

Both tibiotarsal fragments are questionably referred solely on the basis of size.

Remarks. The use of generic names follow Storer (1976a). This material is not diagnostic enough to allow identification to the level of species.

Genus Podilymbus Lesson, 1831Podilymbus cf. P. podiceps

Material. Bone Valley Mining District, Gardinier Mine; UF 65678, distal half of left tibiotarsus; Palmetto Mine; UF 21147, distal half of left tibiotarsus.

Description. Tibiotarsus similar in size and general morphology to that of Podilymbus podiceps. Distinguished from the tibiotarsus of Podiceps by having a smooth medial border of the medial condyle (notched in Podiceps) and a less distinct depressio epicondylaris medialis (very deep in Podiceps). Differs from that of Podilymbus podiceps as follows: Shaft of UF 21147 slightly more robust than in males; tubercle slightly proximal to medial attachment of supratendinal bridge better developed; deeper depressio epicondylaris lateralis than in most specimens. Other characters within range of variation of modern populations of Podilymbus podiceps. Measurements are given in Table 4.5.

Podilymbus sp. A

Material. Mixson Bone Bed local fauna; F:AM FLA 66-1115, proximal end of right tarsometatarsus; F:AM FLA 66-1116, proximal end of left tarsometatarsus.

Remarks. Both specimens are juvenile, at a similar stage of ossification, and have identical morphology; they may represent the same individual. Tarsometatarsal morphology similar to that of Podilymbus podiceps, but differs by being smaller, having a sharper intercondylar knob, and a smooth cranio-dorsal border of the medial cotyla (notched in P. podiceps). Both specimens are too small to correspond to that expected of Podilymbus cf. P. podiceps from the Bone Valley. Measurements given in Table 4.3.

Tribe Podicipedini Storer, 1963

Characters. Absence of a separate canal in the hypotarsus for the tendon of insertion of the M. flexor perforatus digiti II (Storer, 1963). See Murray (1967) for additional osteological characters.

Genus Podiceps Latham, 1787Podiceps sp. indet.

Material. Bone Valley Mining District, Payne Creek Mine; UF 21205, proximal end of left tarsometatarsus.

Remarks. Agrees with Podiceps in hypotarsal configuration (no extra canal). Waterworn and abraded, and is not identifiable to species. Similar in size to Podiceps nigricollis or P. o. occipitalis. (P. auritus much larger).

Tribe indet.

Genus Pliodytes Brodkorb, 1953Pliodytes languisti Brodkorb, 1953

Material. Bone Valley Mining District, Palmetto Mine; PB 299, complete right coracoid (holotype).

Remarks. This species is known only from the holotype. Brodkorb (1953e) states that it possesses characters in common with both Podilymbus and Podiceps but also has its own unique characters. As the tribes of grebes are defined on tarsometatarsal characters (Murray, 1967; Storer, 1963), it is not possible to assign this genus to a tribe. As more fossil material of grebes from the Bone Valley becomes available, this species should be restudied to determine its generic validity and relationships to other species.

Remarks on the Family Podicipedidae.

The family Podicipedidae includes 11 fossil and 19 living species. The earliest certain grebe is Podiceps oligocaenus (Shufeldt), based on a fragmented left femur (missing the proximal end, distal end badly abraded) from the Arikareean John Day Formation, Oregon. It is intermediate in size between the living Podiceps grisegena and P. nigricollis. Although Wetmore (1937) considers it to be correctly allocated to genus, next to nothing can be said about its relationships.

Podiceps pisanus (Portis) based on the distal end of a right humerus, is from the Middle Pliocene (=late Miocene?) of Italy. This species may also be present at the Hemphillian Lee Creek local fauna (Olson, ms.). The only other late Miocene species of grebe now known is Pliodytes lanquisti Brodkorb, discussed above.

There are five species of Pliocene (i.e. Blancan) grebes, all from North America. Podiceps subparvus (L. Miller and Bowman), from the early Blancan San Diego Formation, California, is based on a distal end of a femur. It is approximately the same size as that of the living Podilymbus podiceps and is now known from additional material. Murray (1967) in his review of Pliocene grebes, described one new genus and four new species. Pliolymbus baryosteus Murray, from the Fox Canyon local fauna, Kansas, of Blancan age, is based on the cranial portion of a sternum. Murray (1967) states that this is a small grebe with a robust skeleton but does not suggest any possible relationships between this species and other living or fossil species of grebes. Podiceps discors Murray, also from Fox Canyon, is based on a left tarsometatarsus. It is near the size of Podiceps nigricollis. Murray (1967) also tentatively refers material from the Hagerman local fauna, the San Diego Formation,

California, and the Curtis Ranch, San Pedro Valley, Arizona, to this species. Aechmophorus elasson, Murray, from the Blancan Hagerman local fauna, was described on the distal end of an humerus and an associated left ulna. It is similar to the living A. occidentalis. Podilymbus majusculus Murray, also from the Hagerman local fauna, is based on a nearly complete tarsometatarsus. It is larger than Podilymbus podiceps. He also tentatively refers material from the Rexroad and Saw Rock Canyon local faunas to this species.

Pleistocene species include Podiceps parvus (Shufeldt), based on a lectotype right tarsometatarsus selected by Wetmore (1937) from the Fossil Lake local fauna, Oregon. It is similar to the living P. griseogenus but is appreciably smaller (Howard, 1946). It is also known from a well-core in the Tulane Formation of Kern County, California (Wetmore, 1937). Podiceps dixi Brodkorb is known only from the proximal end of a right carpometacarpus from Reddick, Florida. It was named after the Dixie Lime Products Company which owned the quarry in which it was found (Brodkorb, pers. comm., 1984; etymology omitted in Brodkorb, 1963e). It resembles the living Podiceps auritus, but is somewhat larger (Brodkorb, 1963e). Podilymbus wetmorei Storer is based on a type left tarsometatarsus, also from Reddick, Florida, and from a referred tarsometatarsus and two femora from the Itchtucknee River, Florida. This species is diagnosed as being the size of Podilymbus podiceps but more robust. It is only known from these four elements.

The distribution of fossil grebes from the late Miocene through the early Pliocene of Florida is shown in Table 4.1. Either Podilymbus cf. P. podiceps or Podiceps sp. from Bone Valley could possibly be conspecific with Pliodytes languisti. These species are only known from

a few specimens, none of which are directly comparable. Additional material will eventually determine the validity of these assignments.

The occurrence of Tachybaptus in Florida is not surprising considering the present range of Tachybaptus dominicus throughout the Caribbean. Storer (1976a:124) suggests that T. dominicus has long been separated from its Old World relatives (T. ruficollis subgroup). Supporting this view is the lack of an extra canal in the hypotarsus of T. dominicus (present in T. ruficollis subgroup). Storer (1976a) considers this a derived character of T. dominicus.

The absence of small grebes the size of Tachybaptus from the Bone Valley is probably due to a sampling bias toward large specimens or possibly a general rarity of grebes due to the ecology of the area during the deposition of the Bone Valley Formation.

The presence of Rollandia in the late Miocene of Florida suggests that this genus, like Tachybaptus, had a far greater range in the past.

None of the fossil material of this family now known gives any indication of the higher level systematic relationships of this group. Postulated relationships include the Gaviidae, Hesperornithiformes, Sphenisciformes (Cracraft, 1982), based on primarily foot-propelled swimming adaptations; and the Rhinocerotidae and Eurypygidae, on an apparently unique configuration of the M. longus colli (Zusi and Storer, 1969).

Considering the distribution and diversity of the living species of grebes (cf. Storer, 1963) it is probable that this group originated in either North or South America. Supporting this view is the presence of two genera unique to the Americas (Aechomorphus and Podilymbus) and the diversity of the fossil record (ten out of eleven fossil species occur in

North America). This view is further strengthened by the absence of grebes in the Early Tertiary European fossil localities which have otherwise produced a rich aquatic avifauna (St.-Gérand-le-Puy; Cheneval, 1984; Phosphorites du Quercy; Mourer-Chauvire, 1982). The paucity of knowledge about the evolution of birds in the early Tertiary of South America makes it premature to decide between a North or South American origin, although this did not prevent Storer (1967) from suggesting a South American origin of the family based solely on the diversity of living species.

Table 4.1. Checklist of non-marine avian taxa discussed in the text. Localities where each taxon occurs are given in parentheses -- Love Bone Bed (LOV), McGehee Farm (MCG), Mixson Bone Bed (MIX), Bone Valley (BV), Withlacoochee River 4A (WITH 4A), Manatee County Dam (MD), SR-64, Haile VB (H5B), Haile VI (H6), and Haile XIXA (H19A).

Class Aves

Order Podicipediformes

Family Podicipedidae

- Rollandia sp. (LOV, MIX, MCG)
- Tachybaptus sp. (LOV, MCG)
- Podilymbus cf. P. podiceps (BV)
- Podilymbus sp. A (MIX)
- Podiceps sp. (BV)
- Pliodtytes lanquisti (BV)

Order Pelecaniformes

Family Phalacrocoracidae

- Phalacrocorax sp. A (LOV, MCG, H19A)
- Phalacrocorax wetmorei (BV, MD, SR-64)
- Phalacrocorax cf. idahensis (BV)

Family Anhingidae

- Anhinga grandis (LOV, MCG, H19A)
- Anhinga sp. (BV)

Order Ciconiiformes

Family Ardeidae

- Ardea polkensis (BV)
- Ardea sp. indet. (LOV)
- Egretta sp. indet. (LOV, BV)
- Egretta subfluvia (WITH 4A)
- Ardeola sp. (LOV)
- Nycticorax fidens (MCG)

Family Ciconiidae

- Mycteria sp. (LOV, MCG)
- Ciconia sp. A (LOV)
- Ciconia sp. B (MIX, BV)
- cf. Ciconia sp. C (BV)

Family Platialeidae

- Eudocimus sp. A. (BV)
- Plegadis cf. P. pharangites (LOV)
- Threskiornithinae, genus et species indet. (LOV)

Order Falconiformes (auct.)

Family Vulturidae

- Pliogyps undescribed sp. (LOV)

Table 4.1--continued.

Family Pandionidae

Pandion lovensis (LOV)
Pandion sp. (BV)

Family Accipitridae

Haliaeetus (?) sp. (BV)
Buteo near B. jamaciensis (WITH 4A)
Aquila sp. (BV)
Accipitrid, genus indet. sp. A (LOV)
Accipitrid, genus indet. sp. B (BV)
Accipitrid, genus indet. sp. C (LOV)
Accipitrid, genus indet. (WITH 4A, BV)

Order Anseriformes

Family Anatidae

Dendrocygna sp. (LOV)
Branta sp. A (LOV)
Anserinae, genus indet. sp. B (LOV)
Anserinae, genus indet. sp. C (LOV, BV)
Anserinae, genus indet. sp. D (BV)
Tadorini, genus indet. sp. A (BV)
Anas undescribed sp. A (LOV, MCG)
Anas size near A. acuta (LOV, MCG)
Anatini, genus indet. sp. A (LOV)
Anatini, genus indet. sp. B (LOV)
Aythya sp. A (BV)
Oxyura cf. O. dominica (BV)

Order Galliformes

Family Phasianidae

Meleagridinae, genus indet. (LOV)
Meleagris sp. (BV)

Order Gruiformes (auct.)

Family Gruidae

Grus sp. A (LOV)
Grus sp. B (LOV)
Balearicinae, genus indet. (BV)
Aramornis (cf.) (LOV)

Table 4.1--continued.

Family Rallidae

- Rallus sp. A (LOV)
Rallus sp. B (BV)
Rallus (cf.) sp. C (LOV)
Undescribed genus (LOV, MCG)

Order Charadriiformes

Family Phoenicopteridae

- Phoenicopterus floridanus (BV)
Phoenicopterus sp. A (LOV, MCG)

Family Jacanidae

- Jacana farrandi (LOV, MCG)

Family Scolopacidae

- Limosa ossivallis (BV)
Erolia penepusilla (BV)
Ereunetes rayi (MCG)
Calidris pacis (BV)
"Calidris" sp. indet. 1 (LOV, MCG, BV)
"Calidris" sp. indet. 2 (LOV)
"Calidris" sp. indet. 3 (MCG)
"Calidris" sp. indet. 4 (LOV)
??Actitis sp. indet. 5 (LOV)
??Arenaria sp. indet. 6 (LOV)
Genus indet. sp. indet. 7 (LOV)
Genus indet. sp. indet. 8 (LOV)
?Philomachus sp. (BV)

Order Strigiformes

Family Tytonidae

- Undescribed genus (LOV)

Family Strigidae

- Bubo sp. (BV)

Order Passeriformes

- Suborder indet. sp. A (LOV)
Suborder indet. sp. B (LOV)

Family Fringillidae

- Palaeostruthus eurius (H 6)

Table 4.2. Measurements of humeri and coracoids of the grebes Rollandia, rolland chilensis ($N = 6$, 2 males, 1 female, 3 unsexed), Tachybaptus dominicus ($N = 7$, 4 males, 3 females), and Rollandia sp. from McGehee Farm local fauna. Data are mean \pm standard deviation and range. (*) specimen damaged. Abbreviations defined in methods section.

<u>Measurement</u>	<u>R. r. chilensis</u>	<u>T. dominicus</u>	<u>Rollandia</u> sp.
<u>Humerus</u>			
W-SHAFT	2.67 ± 0.15 $2.5 - 2.8$	2.39 ± 0.15 $2.2 - 2.6$	2.8
D-SHAFT	2.47 ± 0.12 $2.3 - 2.6$	2.11 ± 0.15 $1.9 - 2.3$	2.6
W-DIST	5.35 ± 0.23 $5.1 - 5.7$	5.00 ± 0.31 $4.6 - 5.5$	5.9
<u>Coracoid</u>			
HEAD-FAC	25.45 ± 0.71 $24.3 - 26.2$	21.80 ± 1.57 $20.1 - 24.2$	*24.6
HEAD-IDA	24.50 ± 0.68 $23.3 - 25.3$	21.17 ± 1.26 $19.4 - 23.2$	*23.3
HEAD-CS	7.03 ± 0.23 $6.7 - 7.4$	6.10 ± 0.34 $5.6 - 6.6$	7.6
D-HEAD	2.17 ± 0.10 $2.0 - 2.3$	2.17 ± 0.17 $2.0 - 2.4$	—
W-SHAFT	2.30 ± 0.18 $2.1 - 2.6$	1.94 ± 0.21 $1.7 - 2.3$	2.1
D-SHAFT	1.65 ± 0.10 $1.5 - 1.8$	1.29 ± 0.09 $1.1 - 1.4$	1.7
FAC-IDA	8.53 ± 0.38 $8.2 - 9.1$	7.44 ± 0.41 $7.1 - 8.3$	—
L-GLEN	4.55 ± 0.16 $4.4 - 5.8$	4.31 ± 0.25 $3.8 - 4.5$	5.3

Table 4.3. Measurements of the tarsometatarsi of the grebes Rollandia rolland chilensis ($N = 6$, 2 males, 1 female, 3 unsexed), Podilymbus podiceps ($N = 14$, 7 males, 7 females), Rollandia sp., and Podilymbus sp. A. from the Mixson's Bone Bed. Data are mean \pm standard deviation and range. Abbreviations defined in the methods section.

Measurements	R. r. chilensis	P. podiceps	R. sp.	P. sp.
Tarsometatarsus				
LENGTH	35.58 ± 1.30 33.2 - 36.7	40.15 ± 2.36 36.3 - 44.9	36.4	--
W-PROX	7.00 ± 0.36 6.4 - 7.5	8.09 ± 0.57 7.1 - 8.9	6.7	7.2; 7.5
W-HYPOTS	3.65 ± 0.20 3.3 - 3.8	4.61 ± 0.28 4.1 - 5.1	3.5	4.0; 4.0
TRIII-TRIV	5.20 ± 0.19 5.0 - 5.4	6.57 ± 0.49 5.8 - 7.2	5.6	--
TRII-TRIV	5.22 ± 0.12 5.1 - 5.4	6.24 ± 0.49 5.3 - 7.2	5.2	--
W-TRII	1.55 ± 0.19 1.3 - 1.8	1.96 ± 0.24 1.6 - 2.4	1.7	--
W-TRIII	2.52 ± 0.15 2.3 - 2.7	2.76 ± 0.54 1.5 - 3.3	2.6	--
D-TRIII	3.78 ± 0.21 3.4 - 3.9	5.00 ± 0.41 4.5 - 5.6	4.1	--

Table 4.4. Measurements of the femora of the grebes Rollandia rolland chilensis ($N = 6$, 2 males, 1 female, 3 unsexed), Tachybaptus dominicus ($N = 7$, 4 males, 3 females), and Tachybaptus sp. from the Love Bone Bed. Data are mean \pm standard deviation and range. (*) Specimen damaged. Abbreviations defined in the methods section.

<u>Measurements</u>	<u>R. r. chilensis</u>	<u>T. dominicus</u>	<u>Tachybaptus</u> sp.
<i>Femora</i>			
M-LENGTH	30.73 ± 1.55 $27.9 - 32.0$	25.03 ± 1.53 $23.5 - 27.8$	26.1
L-LENGTH	32.73 ± 1.64 $29.7 - 33.5$	26.81 ± 1.61 $25.1 - 29.7$	27.5
W-SHAFT	2.80 ± 0.15 $2.6 - 3.0$	2.53 ± 0.22 $2.3 - 2.9$	2.6
D-SHAFT	3.18 ± 0.24 $2.8 - 3.4$	2.67 ± 0.30 $2.3 - 3.0$	2.6
W-PROX	7.65 ± 0.39 $7.1 - 8.3$	6.53 ± 0.30 $6.2 - 6.9$	6.8
D-HEAD	3.30 ± 0.24 $3.0 - 3.7$	2.74 ± 0.20 $2.4 - 3.0$	2.8
W-DIST	8.08 ± 0.44 $7.5 - 8.4$	6.84 ± 0.53 $5.9 - 7.4$	*6.0
W-M&LCON	5.97 ± 0.41 $5.4 - 6.4$	4.96 ± 0.40 $4.4 - 5.5$	*5.1
D-LCON	6.03 ± 0.24 $5.7 - 6.4$	4.97 ± 0.37 $4.3 - 5.5$	--
D-MCON	4.40 ± 0.24 $4.1 - 4.7$	3.44 ± 0.26 $3.1 - 3.8$	3.5

Table 4.5. Measurements of the tibiotarsi of the grebes Podilymbus podiceps (N = 14, 7 males, 7 females) and Podilymbus cf. P. podiceps from the Bone Valley Mining District. Data are mean \pm standard deviation and range. (*) Specimen damaged. Abbreviations are defined in the methods section.

<u>Measurements</u>	<u><i>Podilymbus podiceps</i></u>	<u><i>P. cf. podiceps</i></u>
Tibiotarsus		
LENGTH	68.69 \pm 4.31 61.7 - 77.0	--
M-LENGTH	80.17 \pm 5.27 72.4 - 90.2	--
W-SHAFT	4.50 \pm 0.41 3.8 - 5.3	4.6; 4.9
D-SHAFT	3.29 \pm 0.27 2.8 - 3.8	3.5; 3.7
W-PROX-M	7.00 \pm 0.44 6.5 - 7.9	--
W-DIST-CR	7.10 \pm 0.65 6.1 - 7.9	7.2; *7.4
W-DIST-CD	6.04 \pm 0.37 5.2 - 6.5	*6.2; *6.5
D-MCON	6.86 \pm 0.44 6.1 - 7.5	*6.9; 7.4
D-LCON	6.76 \pm 0.49 5.9 - 7.4	7.0; 7.3
D-ICON	4.29 \pm 0.33 3.7 - 4.9	4.4; 4.9

Order Pelecaniformes Sharpe, 1891Family Phalacrocoracidae (Bonaparte, 1853)Genus Phalacrocorax Brisson, 1760

Remarks. The following morphological descriptions are based on the comparisons of a sample of 5 males and 5 females each of Phalacrocorax auritus auritus and P. auritus floridanus, and all available fossil material.

Phalacrocorax sp. A.

Material. Love Bone Bed local fauna; UF 25735, distal ends left humeri; UF 29661, distal end right ulna; UF 25877, distal end left tibiotarsus; UF 25861, distal end right tarsometatarsus (badly worn, tentatively referred); UF 25933, distal end left tarsometatarsus.

McGehee Farm local fauna; UF 11569, complete left coracoid; UF 31779, sternal end left coracoid; UF 12351, distal end right humerus; UF 4107, proximal end right ulna; UF 9492, proximal end right ulna (questionably referred); UF 31778, proximal end right carpometacarpus; UF 11105, distal end left carpometacarpus; UF 29746, complete left tarsometatarsus; UF 31777, proximal end right tarsometatarsus. PB 7964, proximal end left carpometacarpus.

Haile XIXA; UF 29774, proximal end left humerus; UF 47340, proximal end right carpometacarpus.

Description. Coracoids from McGehee Farm differ from those of both subspecies of Phalacrocorax auritus (auritus and floridanus) examined, and from P. wetmorei by having a more elliptical facies articularis clavicularis, a more robust shaft in relation to the length of coracoid, the brachial tuberosity more undercut, the impression for the attachment

of the coraco-brachialis more distinct, and in medial view, the shaft more rotated ventrally.

Distal end of the humeri of the fossil species is generally smaller than that of females of P. a. floridanus, and the shaft more slender (much smaller than P. a. auritus). Other characters are within the range of variation of P. auritus. Differs from the humeri of P. wetmorei by being smaller, having a more shallow fossa brachialis of a different angle and a much wider attachment of the anterior articular ligament (=tuberculum supracondylare ventrale).

The two ulnae that are sufficiently preserved to make comparisons (UF 29662, UF 4107) appear small, about the size of small females of P. a. floridanus. Characters are within the range of variation of this species.

Carpometacarpus larger than that of the largest male P. a. auritus. Process of metacarpal I more nearly square than in that of P. auritus. Shaft of metacarpal II more robust and angular; anterior carpal facet not extending up the carpal trochlea as in P. auritus. Pollical facet with a small papilla.

Tibiotarsus indistinguishable from that of small females of P. a. floridanus.

Tarsometatarsus description based on UF 29746 (UF 25933 broken and badly worn; UF 31777 missing distal half, but both agree with UF 29746 in all discernable characters). Tarsometatarsus short, about equal to that of females of P. a. floridanus. Transverse width of shaft very narrow. Lateral face of shaft much more flattened than P. auritus, causing the posterior intermuscular line to be on the lateral edge of the shaft. Proximal end narrow, lateral calcaneal ridge more narrow and elongate

than in P. auritus. Posterior opening of the lateral proximal vascular foramen is located lateral to the ridge extending down from the lateral calcaneal ridge. This ridge not extending as far down the shaft as in P. auritus.

Remarks. If the carpometacarpus above is correctly assigned to the same species as is represented by the other skeletal elements, then this cormorant is quite different in proportions than Phalacrocorax auritus and related species such as Phalacrocorax wetmorei.

Phalacrocorax wetmorei Brodkorb, 1955

Material. This material is very well represented in the Bone Valley Fauna. Only Florida State Museum and Florida State Geological specimens are included in the following referred material section. Material accessioned into the Florida State Museum collections after 26 April 1984 has not been included in the list of referred specimens; material accessioned after 5 March 1984 has not been included in the tables of measurements. Additional material from Bone Valley (type material) is listed in Brodkorb (1955a).

Manatee County Dam Site.--UF 11916, distal end right humerus.

SR-64 local fauna.--UF 67805, complete left coracoid; UF 64143, humeral end left coracoid; UF 64144, humeral end right coracoid; UF 64146, humeral end right scapula; UF 64145, partial sternum; UF 64147, proximal end right tibiotarsus; UF 64148, UF 64149, distal ends left tarsometatarsi.

Bone Valley Mining District, Brewster Mine.--UF 61987, humeral end right coracoid; UF 61988, distal end right tarsometatarsus; UF 65691, proximal end left ulna.

Bone Valley Mining District, Chicora Mine.--UF 29733, humeral end left coracoid.

Bone Valley Mining District, Fort Green Mine.--UF 61958, associated (?) partial skeleton; UF 58062, right quadrate; UF 60047, caudal portion left mandible; UF 53912, caudal portion right mandible; UF 57248, sternal fragment with coracoidal sulci; UF 52415, UF 53938, proximal ends right scapulae; UF 53873, proximal end left scapula; UF 62025, complete left coracoid; UF 52413, UF 57332, UF 55838, UF 57246, UF 58058, UF 61960, UF 65711, humeral ends right coracoids; UF 53913, UF 55872, UF 57331, UF 58059, UF 58339, UF 61961, UF 65655, humeral ends left coracoids; UF 52414, UF 61962, UF 65656, sternal ends right coracoids; UF 53934, UF 55831, UF 55875, UF 61963, sternal ends left coracoids; UF 55810, UF 55811, UF 58378, UF 61964, proximal end right humeri; UF 58304, UF 60048, proximal ends left humeri; UF 53937, shaft left humerus; UF 52410, UF 53914, UF 60050, UF 65657, distal ends right humeri; UF 55865, UF 58060, UF 58338, UF 58419, UF 58420, UF 60049, distal ends left humeri; UF 55867, UF 57242, UF 58061, UF 60051, UF 65712, proximal ends right ulnae; UF 55866, UF 61965, proximal ends left ulnae; UF 57243, UF 57247, UF 57249, UF 60052, UF 61966, distal ends right ulnae; UF 52411, UF 55812, UF 55871, UF 57334, UF 57335, UF 58340, distal ends left ulnae; UF 55813, UF 55832, UF 55869, UF 60053, UF 65661, proximal ends right carpometacarpi; UF 52412, UF 55833, UF 55834, UF 57333, UF 58418, UF 61967, UF 61968, UF 61969, UF 58407, distal ends right carpometacarpi; UF 61959, partial synsacrum; UF 55814, UF 60054, complete right femora; UF 57336, complete left femur; UF 57244, proximal end right femur; UF 53872, UF 53872, UF 55873, UF 55874, UF 57337, UF 60055, UF 61970, UF 55835, distal ends right femora; UF 57391, UF 61971, distal ends left femora; UF

55868, proximal end right tibiotarsus; UF 55836, UF 57245, UF 60056, proximal end left tibiotarsus; UF 55804, UF 57250, distal ends right tibiotarsi; UF 53935, UF 55863, UF 55864, UF 57357, UF 58305, UF 60057, UF 60058, UF 65713, distal ends left tibiotarsi; UF 55860, nearly complete left tarsometatarsus; UF 52416, UF 52417, UF 52418, UF 55837, UF 58067, proximal end right tarsometatarsi; UF 55870, UF 58421, UF 61972, proximal ends left tarsometatarsi; UF 53889, UF 53936, UF 55815, UF 57251, UF 58306, UF 58341, distal ends right tarsometatarsi; UF 58342, UF 60059, UF 65658, distal end left tarsometatarsi.

Bone Valley Mining District, Gardiner Mine.--UF 58438, caudal portion right mandible; UF 61998, right clavicle; UF 61999, proximal end right scapula; UF 62000, proximal end left scapula, UF 65667, complete left coracoid; UF 58278, UF 58279, UF 58439, UF 58440, UF 62001, UF 65669, humeral ends right coracoids; UF 58277, UF 58280, UF 58446, UF 58447, UF 58469, UF 62002, UF 62003, UF 62004, UF 65668, humeral ends left coracoids; UF 58448, sternal end left coracoid; UF 58470, UF 62005, proximal ends right humeri; UF 58441, UF 58471, distal ends right humeri; UF 58449, UF 58472, UF 62006, distal ends left humeri; UF 58281, UF 58442, UF 62007, UF 65670, proximal end right ulnae; UF 62008; proximal end left ulna; UF 57307, UF 58285, UF 58286, UF 65671, distal end right ulnae; UF 58282, UF 58283, UF 58284, UF 65672, UF 65749, distal end left ulnae; UF 58443, proximal end right carpometacarpus; UF 58287, proximal end left carpometacarpus; UF 58303, UF 58282, distal ends left carpometecarpi; UF 58450, complete left femur; UF 58451, proximal end left femur; UF 58473, distal end right femur; UF 57311, proximal end left tibiotarsus; UF 58290, UF 58444, UF 58445, UF 58474, UF 58475, distal ends right tibiotarsi; UF 58289, UF 58452, UF 58453, UF 62009, UF 62010,

UF 62011, UF 62012, distal ends left tibiotarsi; UF 65673, complete right tarsometatarsus; UF 58478, UF 62013, proximal end right tarsometatarsi; UF 58291, UF 58292, proximal end left tarsometatarsi; UF 58293, UF 58476, UF 58477, UF 65674, distal ends right tarsometatarsi; UF 57310, distal end left tarsometatarsus.

Bone Valley Mining District, Palmetto Mine.—UF 21058, sternal fragment with coracoidal sulci; UF 13225, humeral end left coracoid; UF 21143, shaft left coracoid; UF 21115, shaft right coracoid; UF 21146, distal end right humerus; UF 2973⁴, distal end left humerus; UF 13231, UF 29740, distal ends right ulnae; UF 21091, UF 21120, proximal ends right carpometacarpi, UF 21068, UF 21072, proximal ends left carpometacarpi; UF 21131, distal end right carpometacarpus; UF 49090, complete right femur; UF 12352, complete left femur; UF 29735, UF 49091, proximal ends left tarsometatarsi; UF 12868, distal end right tarsometatarsus.

Bone Valley Mining District, New Palmetto Mine.—UF 49691, UF 49692, vertebrae (questionably referred), UF 49693, complete right femur; UF 49694, complete left tarsometatarsus.

Bone Valley Mining District, North Palmetto Mine.—UF 49097, humeral end left coracoid; UF 49098, humeral end right coracoid.

Bone Valley Mining District, Southwest Palmetto Mine.—UF 49093, humeral end right coracoid.

Bone Valley Mining District, Hookers Prairie Mine.—UF 49690, complete right femur.

Bone Valley Mining District, Kingsford Mine.—UF 21186, humeral end left coracoid; UF 52971, distal end right humerus; UF 13212, distal end left humerus; UF 21185, proximal end right tibiotarsus.

Bone Valley Mining District, Payne Creek Mine.--UF 29741, UF 57304, humeral ends right coracoids; UF 21203, proximal end left carpometacarpus; UF 29742, distal end right carpometacarpus.

Bone Valley Mining District, Swift Mine.--UF 55883, distal end right tibiotarsus; UF 17687, distal end right tatsometatarsus.

Bone Valley Mining District, specific locality unknown.--UF 61549, caudal portion left mandible; UF 61550, nearly complete right coracoid; UF 61553, nearly complete left coracoid; UF 61554, UF 61555, humeral ends left coracoids; UF 61551, humeral end right coracoid; UF 61552, sternal end right coracoid; UF 61556, sternal end left coracoid; UF 61557, UF 61558, proximal end right humerus; UF 61559, UF 61560, proximal end left humeri; UF 61561, distal end right humerus; UF 61562, UF 61563, UF 61564, UF 61565, UF 61566, UF 61567, UF 61568, UF 61569, distal end left humeri; UF 61570, UF 61571, proximal end left ulnae; UF 61572, UF 61573, UF 61574, distal ends right ulnae; UF 61575, distal end left ulna; UF 61578, nearly complete left carpometacarpus; UF 61576, UF 61577, proximal ends right carpometacarpi; UF 61579, proximal end left carpometacarpus; UF 61596, complete left femur; UF 61580, proximal end left tibiotarsus; UF 61581, UF 61582, UF 61583, UF 61584, distal ends right tibiotarsi; UF 61585, UF 61586, UF 61587, distal ends left tibiotarsi; UF 61588, nearly complete left tarsometatarsus; UF 61589, UF 61590, UF 61591, UF 61592, proximal end left tarsometatarsus; UF 61593, distal end right tarsometatarsus; UF 61594, UF 61595, distal ends left tarsometatarsi.

Bone Valley Mining District, specific locality unknown (FGS collection).--V 7311, proximal end left humers; V 7313, distal end left humerus; V 7309, distal end left ulna; V 7310, proximal end left carpometacarpus; V 7312, distal end left femur.

Description. Scapula within range of variation of that of *Phalacrocorax auritus*.

Coracoids appear to be well within the range of variation of those of *P. auritus*. The characters used by Brodkorb (1955a: 12) "anterior intermuscular line situated farther laterad" applies only at the extreme sternal end of the coracoid. This line does not swing mediad; instead it curves little as it extends down the shaft. Differs from UF 11569 from McGehee by characters cited above. Coracoids from SR-64 are indistinguishable from those of *Phalacrocorax wetmorei* from Bone Valley.

The two characters of the humerus used by Brodkorb (1955a:12) "the head of humerus shallower" and "condyles averaging less deep" do not hold when a large series of specimens are measured (Table 4.7). Brodkorb's statements that the pneumatic fossa is narrow (slightly) and deeper are supported. This is especially apparent by having a small, but deep fossa paralleling the crus ventrale fossae. In *P. wetmorei* the pneumatic fossa is perforated by several pneumatic foramina, but it is rarely perforated in *P. auritus*. In the few specimens of *P. auritus* in which these foramina are present, they are very minute. Ligamental furrow (= ligamental sulcus) does not appear to be relatively longer when compared against a series of both sexes and subspecies of *P. auritus*. The distal end of the humerus of *P. wetmorei* tends to be narrower, with a more elongated attachment for the anterior articular ligament (= tuberculum supracondylare ventrale) ending proximally in a narrower crest than in the modern specimens of *P. auritus*. Measurements of ulnae are given in Table 4.7.

Carpometacarpi of *P. wetmorei* are about as robust as those of females of *P. f. floridanus*. The process of metacarpal I is slightly

more produced. Fovea carpalis caudalis deeper in P. wetmorei than in P. auritus.

The femora are similar, except that the popliteal fossa is generally less excavated than in P. auritus. Brodkorb's statement that the femur is longer and narrower than that of P. auritus is not supported by the larger sample size now available.

Tibiotarsus with no obvious qualitative morphological differences, but see Table 4.10 for a few minor quantitative differences.

Tarsometatarsus with a lateral face flat, similar to but not as extreme as, that found on specimens from the Love Bone Bed local fauna. Other characters similar. See Table 4.11 for measurements.

Remarks. See comments under Family Remarks (below) pertaining to P. auritus and related species.

Phalacrocorax cf. P. idahensis

Material. Bone Valley Mining District, Palmetto Mine (locality 2 of Brodkorb, 1955); PB 311, proximal end left ulna.

Remarks. This proximal ulna (PB 311) is larger than that of other specimens of P. wetmorei presently known from Bone Valley. Since it was first reported by Brodkorb (1955), it has been additionally damaged in transport and is now barely diagnostic at the generic level. Unless additional material becomes available, the status of this enigmatic record in Florida will probably never be satisfactorily resolved.

Remarks on the Family Phalacrocoracidae.

The cormorants have an extensive fossil record. Brodkorb (1963c) lists 23 paleospecies; subsequently eight more have been described, or are in the process of being described. Most have been referred to the

genus Phalacrocorax (presently with 26 paleospecies), many without extensive comparisons with other recent and fossil species to determine the variability of the characters used. It would be desirable to revise the paleospecies of Phalacrocorax and integrate this extensive fossil record with the recent species to produce a phylogeny of the family. There are large amounts of fossil material available, permitting analysis of variation of several fossil species (e.g. P. wetmorei, P. oweri, etc.), a recent descriptive osteological study (Ono, 1980), and papers identifying osteological characteristics and proportions of the various subgenera of cormorants (Howard, 1932a, 1965; Brodkorb and Mourer-Chauvire, 1984). However, such a revision is beyond the scope of this dissertation.

Species listed by Brodkorb (1963c) that are not cormorants include all species of the genus Graculavus (moved to Charadriiformes, Olson and Parris, ms), Actiornis anglicus (not a cormorant, nor ibis, Olson, 1981b), and Phalacrocorax mediterraneus (Gruiformes, Family Bathornithidae = Paracrax antiqua, Cracraft, 1971).

The earliest cormorants appear in the early Miocene. Phalacrocorax subvolans Brodkorb from the mid-Hemingfordian Thomas Farm local fauna, Florida, is known only from a proximal humerus. It is currently under study (Becker, in prep.). Phalacrocorax marinavis Shufeldt from the Arikareean John Day Formation, Oregon, is known from a humerus, ulna, tarsometatarsus, and part of a femur. It is somewhat smaller than P. carbo but is reported to be allied with this species. Phalacrocorax miocaenus (Milne-Edwards) from the Aquitanian of Langy, Vaumas, St.-Gérand-le-Puy, and Montaigu, France, is known from most skeletal elements. It was moved to a new genus Nectornis and is said to share

characters with Anhinga (Cheneval, 1984). Phalacrocorax littoralis (Milne-Edwards) from the Aquitanian of St.-Gérand-le-Puy, France, and from Germany was based on a coracoid and a few other skeletal elements. It seems to be related to P. aristotelis. Phalacrocorax anatolicus Mourer-Chauvire from the lower or middle Miocene (probably Helvétian) of Bes-Konak, Turkey, was described from a coracoid and most of a forelimb. It appears to be related to the fossil species P. littoralis, P. miocaenus, and to the recent P. aristotelis.

Phalacrocorax leptopus Brodkorb from the Clarendonian and Hemphillian localities of Juntura, Oregon, is based on a coracoid, tarsometatarsus, and scapula. It is a small species and resembles the fossil P. littoralis. It is in need of additional comparisons to elucidate its relationships.

Phalacrocorax femoralis L. Miller from the Barstovian or Clarendonian Calabasas local fauna, California, is based on most of a skeleton, preserved in a slab of fine-grained shale. It is the size of P. penicillatus, but Miller (1929) asserts that this species does not appear closely related to any living species. Phalacrocorax laetus Kurochkin and Ganya from the upper Miocene of Moldavia, is based on the proximal half of a right femur. It appears closest to the living P. pygmaeus.

Phalacrocorax praecarbo Ammon was described from the upper Miocene Brown Coal Formation, near Württemburg, Germany, on the humeral end of a coracoid. Brodkorb (1980) has moved Ardea brunhuberi Ammon (figured in Ammon, 1911), based on a proximal end of a carpometacarpus to this species and emended the name to P. brunhuberi (Ammon, 1918; cited as 1911 in Brodkorb, 1980). Olson (ms) also moves Botaaurites auritus Ammon,

based on a cervical vertebra to P. brunhuberi. Phalacrocorax intermedius (Milne-Edwards) from the Oreleanian of Orleanais, France was described from a proximal end of a humerus. Phalacrocorax brunhuberi may be synonymous with P. intermedius; only slightly smaller size and slightly younger age prevented Brodkorb (1980) from placing it in synonymy with this species.

Phalacrocorax ibericum Villalta, probably from the Lower Pontian of Spain, is based on the distal end of a humerus. Villalta states that this cormorant is smaller than the other Aquitanian cormorants of Europe (P. littoralis, P. miocenaeus, and P. intermedius) and is close to the living P. carbo.

Phalacrocorax goletensis Howard from the late Hemphillian or early Blancan La Goletia local fauna, Michoacan, Mexico, is known from a coracoid (type) and a referred distal humerus. It is possibly ancestral to P. olivaceus.

Five species, all said to be ancestral to P. auritus, have been described from the late Hemphillian to Mid-Pleistocene of North America. Phalacrocorax wetmorei Brodkorb, described from the late Hemphillian Bone Valley District, Florida, is known from all major skeletal elements. See additional remarks above. Phalacrocorax kennelli Howard from the Blancan San Diego Formation, was described on a partial coracoid, a humerus, a furculum, and vertebrae. It agrees in size with P. pelagicus and P. penicillatus. In morphology, the fossil species resembles P. auritus or P. pelagicus (Howard, 1949). Phalacrocorax idahensis (Marsh) from the Hemphillian Castle Creek, Idaho, is based on a proximal carpometacarpus. Murray (1970) referred additional material to and redescribed this species from the (Blancan) Hagerman local fauna. Phalacrocorax macer

Brodkorb from the (Blancan) Hagerman local fauna, Idaho, was originally described on a carpometacarpus. Murray (1970) also redescribed this species based on additional material. Phalacrocorax macropus (Cope) from the Mid-Pleistocene Fossil Lake local fauna, Oregon, was described on a tarsometatarsus. Howard (1946) referred many other specimens to this species.

I do not believe that all these species are valid and are correctly assigned to the ancestral lineage of P. auritus. The morphological differences among the fossil species are comparable to those among subspecies of modern P. auritus. It is very possible that like modern cormorants that show geographic size variations (Palmer, 1962), the fossil species are simply conspecific geographical variants. If this can be demonstrated, then each of these fossil species should be maintained as subspecies of the senior synonym, Phalacrocorax macropus (Marsh).

Valenticarbo praetermissus Harrison from the late Pliocene to early Pleistocene of Siwalks, India, is based on a 100-year-old plaster cast of a proximal end of a tarsometatarsus, lacking the hypotarsus. It is very doubtful that this genus is valid (Olson, ms.). I am unaware of the relationship of this supposed species.

Pliocarbo longipes Tugarinov from the early Pliocene of the Ukraine was described from a worn tarsometatarsus and a referred femur. Olson (ms) notes that although the size and proportions of the tarsometatarsus are different from typical cormorants, the illustrations are too poor for even a positive familial verification.

Phalacrocorax destenfani Regalia from the Mid-Pliocene (Ruscinian?) of Orciano, Pisano, Italy, was described from most major skeletal elements. Phalacrocorax mongoliensis Kurochkin from the upper Pliocene

of Mongolia is based on the distal epiphysis of a left femur.

Phalacrocorax reliquus Kurochkin from the middle Pliocene of western Mongolia, is based on the distal epyphysis of a right humerus. It has the same dimensions as P. pelagicus. The relationships of these cormorants have not been determined.

Phalacrocorax rogersi Howard from the Pliocene Veronica Springs Quarry, California, is known only from the type coracoid. It is a large species and appears close to P. perspicillatus and P. pelagicus.

Phalacrocorax owrei Brodkorb and Mourer-Chauvire, from the lower Pleistocene of Olduvai Gorge, Tanzania, is known from nearly all skeletal elements. It has been assigned to the subgenus Stictocarbo, although its tarsometatarsus is rather similar to P. fuscicollis (subgenus Phalacrocorax). Phalacrocorax tanzaniae Harrison and Walker from the Pleistocene Bed II of Olduvai Gorge, Tanzania, was described from a tarsometatarsus and appears close to P. carbo. Phalacrocorax pampeanus Moreno and Mercerat from the upper Pleistocene Lujan local fauna, Argentina, was described from the proximal end of a humerus. It is very close to P. olivaceus and may be ancestral to this recent species (Howard, 1965). Phalacrocorax gregorii and P. yetustus DeVis from the upper Pleistocene localities near Lake Eyre, South Australia, were described from many elements.

Table 4.6. Measurements of coracoids and scapulae of the cormorants *Phalacrocorax auritus auritus* ($N = 14$, 7 males, 7 females), *Phalacrocorax auritus floridanus* ($N = 18$, 9 males, 9 females), *Phalacrocorax wetmorei*, and *Phalacrocorax* sp. from the McGehee Farm local fauna. Data are mean \pm standard deviation, (N), and range. Abbreviations are defined in methods section.

Measurements	<i>P. a. auritus</i>	<i>P. a. floridanus</i>	<i>P. wetmorei</i>	<i>Phalacrocorax</i> sp.
Coracoid				
HEAD-IDIA	64.35 \pm 2.79 59.3 \pm 67.9	60.87 \pm 2.83 56.3 \pm 65.6	64.38 \pm 2.60 (4) 60.7 \pm 66.8	59.3
HEAD-CS	22.74 \pm 1.08 20.1 \pm 23.8	21.16 \pm 1.14 19.1 \pm 23.7	22.40 \pm 0.64 (41) 21.1 \pm 23.8	21.8
D-HEAD	8.28 \pm 0.47 7.6 \pm 9.0	7.69 \pm 0.58 6.5 \pm 8.7	8.02 \pm 0.50 (40) 7.4 \pm 9.2	7.0
W-SHAFT	5.26 \pm 0.33 4.9 \pm 6.0	4.84 \pm 0.46 4.1 \pm 5.5	5.26 \pm 0.38 (7) 4.8 \pm 5.8	5.5
D-SHAFT	6.21 \pm 0.47 5.5 \pm 7.2	5.36 \pm 0.66 4.1 \pm 6.4	5.16 \pm 0.30 (7) 4.7 \pm 5.6	5.8
IDA-PP	48.25 \pm 2.61 43.4 \pm 51.4	46.04 \pm 2.07 42.5 \pm 49.2	48.53 \pm 2.32 (4) 45.1 \pm 50.2	43.6
L-GLEN	12.38 \pm 0.46 11.5 \pm 13.3	11.68 \pm 0.57 10.6 \pm 12.6	12.29 \pm 0.46 (44) 11.3 \pm 13.2	12.0
Scapula				
W-NECK	6.05 \pm 0.41 5.4 \pm 6.8	5.34 \pm 0.37 4.3 \pm 6.0	5.83 \pm 0.38 (12) 5.1 \pm 6.4	—
ACR-GLN	16.46 \pm 0.98 14.7 \pm 18.1	15.26 \pm 0.94 13.4 \pm 17.3	15.54 \pm 1.35 (8) 12.5 \pm 16.6	—

Table 4.7. Measurements of the humeri and ulnae of the cormorants *Phalacrocorax auritus* ($N = 14$, 7 males, 7 females), *Phalacrocorax auritus floridanus* ($N = 18$, 9 males, 9 females), *Phalacrocorax wetmorei* from the Bone Valley Mining District, Manatee Co. Dam (M), and Haile XIXA (H), and *Phalacrocorax* sp. from McGehee Farm and the Love Bone Bed. Data are mean \pm standard deviation, (N), and range. Abbreviations are defined in the methods section.

Measurements	<i>P. a. auritus</i>	<i>P. a. floridanus</i>	<i>P. wetmorei</i>	MCD/HXIA	McGehee	LBB
Humerus						
W-SHAFT	8.04 \pm 0.50 7.2 - 8.9	7.16 \pm 0.47 6.3 - 7.9	8.09 \pm 0.36 (18) 7.1 - 8.6	—	7.4	7.8
D-SHAFT	6.85 \pm 0.44 6.0 - 7.7	6.16 \pm 0.37 5.5 - 6.8	6.22 \pm 0.33 (18) 5.4 - 7.0	—	6.2	6.3
W-PROX	22.91 \pm 1.02 21.0 - 24.6	21.52 \pm 1.34 19.7 - 24.1	23.19 \pm 0.88 (16) 21.5 - 24.8	20.4 (H)	—	—
D-PROX	7.47 \pm 0.25 7.1 - 8.0	6.80 \pm 0.50 5.9 - 7.7	6.97 \pm 0.25 (18) 6.3 - 7.3	6.4 (H)	—	—
D-HEAD	11.10 \pm 0.54 10.5 - 11.8	10.21 \pm 0.75 8.8 - 11.3	10.85 \pm 0.18 (10) 10.6 - 11.1	9.5 (H)	—	—
L-DELTOID	36.22 \pm 1.69 33.4 - 38.8	34.31 \pm 1.92 31.4 - 37.6	36.89 \pm 1.75 (11) 34.1 - 39.3	34.2 (H)	—	—
W-DIST	15.94 \pm 0.52 15.4 - 16.8	14.79 \pm 0.91 12.6 - 16.4	15.63 \pm 0.43 (37) 14.9 - 16.8	15.4 (M)	15.2	13.2; 14.9
D-DIST	10.88 \pm 0.59 10.0 - 11.9	10.15 \pm 0.68 8.9 - 11.8	10.29 \pm 0.36 (35) 9.4 - 11.1	10.2 (M)	9.9	9.5 9.5
D-ENTEP	7.25 \pm 0.25 7.2 - 7.9	7.10 \pm 0.45 6.3 - 8.1	7.18 \pm 0.25 (39) 6.7 - 7.7	7.3 (M)	6.8	6.4; 6.9

Table 4.7--continued

<u>Measurements</u>	<u>P. a. auritus</u>	<u>P. a. floridanus</u>	<u>P. wetmorei</u>	<u>MCD/HXIXA</u>	<u>McGehee</u>	<u>LBB</u>
Ulna W-PROX	11.95 ± 0.41 11.4 - 12.7	11.11 ± 0.69 9.8 - 12.4	11.52 ± 0.42 (27) 10.6 - 12.8	--	11.1	--
D-LENGTH	15.74 ± 0.83 14.5 - 17.2	14.19 ± 1.12 12.3 - 16.4	14.73 ± 0.70 (22) 13.3 - 16.0	--	14.1	--
D-PROX	12.50 ± 0.58 11.5 - 13.5	11.31 ± 0.90 9.8 - 13.0	11.61 ± 0.43 (27) 10.5 - 12.3	--	11.2	--
ECON	8.26 ± 0.36 7.8 - 8.9	7.62 ± 0.48 6.9 - 8.5	8.04 ± 0.26 (27) 7.5 - 8.6	--	--	8.0
CPTB	8.95 ± 0.27 8.3 - 9.3	8.37 ± 0.46 7.5 - 9.0	8.46 ± 0.37 (27) 7.7 - 9.0	--	--	8.4
ECON-CPTB	11.15 ± 0.50 10.3 - 11.9	10.38 ± 0.49 9.7 - 11.3	10.70 ± 0.35 (28) 9.7 - 11.3	--	--	10.6
ECON-ICON	6.29 ± 0.27 5.8 - 6.7	5.83 ± 0.23 5.4 - 6.3	6.47 ± 0.15 (26) 6.2 - 6.7	--	--	6.2

Table 4.8. Measurements of carpometacarpri of the cormorants Phalacrocorax auritus ($N = 14$, 7 males, 7 females), Phalacrocorax auritus floridanus ($N = 18$, 9 males, 9 females), Phalacrocorax wetmorei, from the Bone Valley, and Phalacrocorax species from McGehee Farm and Haile XIXA. Data are mean \pm standard deviation, (N), and range. Abbreviations defined in methods section.

Measurements	<u>P. a. auritus</u>	<u>P. a. floridanus</u>	<u>P. wetmorei</u>	<u>Haile XIXA</u>	<u>McGehee</u>
Carpometacarpus LENGTH	69.01 \pm 2.49 63.8 - 73.3	66.51 \pm 2.74 62.6 - 70.1	69.6 (1)	—	—
W-PROX	7.79 \pm 0.25 7.4 - 8.1	7.31 \pm 0.36 6.7 - 8.0	6.93 \pm 0.36 (26) 5.9 - 7.6	6.8	8.3
W-CARPAL	6.29 \pm 0.30 5.9 - 6.9	6.00 \pm 0.27 5.5 - 6.4	6.04 \pm 0.26 (28) 5.4 - 6.4	6.1	5.6; 7.2
D-PROX	13.30 \pm 0.40 12.7 - 14.1	12.54 \pm 0.51 11.5 - 13.3	13.68 \pm 0.39 (24) 13.1 - 14.2	12.6	12.9; 16.4
L-MCI	10.64 \pm 0.47 9.4 - 11.3	10.06 \pm 0.68 8.9 - 11.4	9.87 \pm 0.38 (23) 9.3 - 10.5	9.1	9.7; 11.5
D-SHAFT	3.54 \pm 0.19 3.3 - 3.9	3.18 \pm 0.17 2.9 - 3.4	3.69 \pm 0.34 (8) 3.3 - 4.3	—	4.6
W-SHAFT	4.69 \pm 0.23 4.3 - 5.2	4.34 \pm 0.21 4.0 - 4.8	4.68 \pm 0.12 (8) 4.6 - 4.9	—	5.4
D-DIST	5.01 \pm 0.23 4.6 - 5.3	4.71 \pm 0.29 4.0 - 5.2	4.91 \pm 0.33 (8) 4.4 - 5.4	—	4.8
W-DIST	7.44 \pm 0.22 7.1 - 7.7	7.08 \pm 0.37 6.3 - 7.7	7.42 \pm 0.21 (9) 7.2 - 7.8	—	7.1

Table 4.9. Measurements of the femora of the cormorants *Phalacrocorax auritus auritus* (N = 14, 7 males, 7 females), *Phalacrocorax auritus floridanus* (N = 18, 9 males, 9 females), and *Phalacrocorax wetmorei*, from the Bone Valley Mining District. Data are mean \pm standard deviation, (N), and range. Abbreviations are defined in the methods section.

Measurements	P. a. auritus	P. a. floridanus	P. wetmorei
Femur			
M-LENGTH	54.89 \pm 2.40 49.5 - 58.7	52.12 \pm 3.15 43.2 - 57.2	55.46 \pm 1.58 (9) 53.3 - 59.2
L-LENGTH	56.58 \pm 2.63 50.1 - 60.0	54.03 \pm 2.51 49.4 - 59.1	57.58 \pm 1.45 (12) 55.7 - 61.0
W-SHAFT	6.48 \pm 0.36 5.6 - 7.1	5.94 \pm 0.38 5.2 - 6.5	6.49 \pm 0.29 (17) 5.9 - 7.0
D-SHAFT	8.15 \pm 0.50 6.9 - 8.6	7.38 \pm 0.46 6.7 - 8.4	8.04 \pm 0.41 (17) 7.3 - 9.0
W-PROX	16.13 \pm 0.60 15.5 - 17.4	14.56 \pm 0.85 13.2 - 16.2	15.43 \pm 0.59 (21) 14.5 - 16.7
D-HEAD	7.02 \pm 0.33 6.4 - 7.6	6.55 \pm 0.33 6.0 - 7.3	6.76 \pm 0.28 (16) 6.3 - 7.2
W-DIST	15.71 \pm 0.59 14.9 - 16.6	14.93 \pm 0.84 13.3 - 16.5	15.11 \pm 0.47 (17) 14.4 - 16.0
W-M&LCON	12.21 \pm 0.65 11.3 - 13.2	11.38 \pm 0.77 10.0 - 13.0	11.59 \pm 0.39 (14) 10.8 - 12.3
W-LCON	3.34 \pm 0.27 3.0 - 3.9	3.02 \pm 0.33 2.5 - 3.6	2.99 \pm 0.20 (13) 2.7 - 3.3
W-L&FCON	7.25 \pm 0.25 6.9 - 7.7	6.74 \pm 0.41 5.8 - 7.4	6.85 \pm 0.32 (15) 6.4 - 7.5
D-FCON	8.81 \pm 0.47 8.3 - 9.5	8.40 \pm 0.50 7.5 - 9.2	8.68 \pm 0.40 (17) 8.1 - 9.4
D-LCON	10.36 \pm 0.37 9.8 - 11.1	9.78 \pm 0.57 8.7 - 10.5	10.14 \pm 0.37 (14) 9.6 - 10.8
D-MCON	9.05 \pm 0.34 8.4 - 9.7	8.59 \pm 0.48 7.6 - 9.4	8.68 \pm 0.33 (18) 8.1 - 9.4

Table 4.10. Measurements of the tibiotarsi of the cormorants Phalacrocorax auritus auritus ($N = 14$, 7 males, 7 females), Phalacrocorax auritus floridanus ($N = 18$, 9 males, 9 females), Phalacrocorax wetmorei, from the Bone Valley Mining District, and Phalacrocorax species from the Love Bone Bed. Data are mean + standard deviation, (N), and range. Abbreviations are defined in the methods section.

Measurements	P. a. auritus	P. a. floridanus	P. wetmorei	Phalacrocorax sp.
Tibiotarsus				
FIBULAR	43.18 + 1.99 38.5 - 45.8	41.26 + 1.94 36.7 - 43.9	37.7 (1)	---
W-SHAFT	6.92 + 0.22 6.6 - 7.4	6.63 + 0.28 6.0 - 7.1	7.02 + 0.25 (5) 6.6 - 7.2	---
D-SHAFT	5.41 + 0.46 4.8 - 6.5	4.88 + 0.34 4.3 - 5.4	5.14 + 0.09 (5) 5.0 - 5.2	---
W-PROX-M	11.70 + 0.67 10.7 - 12.7	10.84 + 0.81 8.9 - 12.2	11.70 + 0.80 (5) 10.5 - 12.7	---
D-PROX	17.09 + 0.75 16.2 - 18.4	15.87 + 0.79 14.1 - 17.6	17.22 + 0.78 (5) 16.5 - 18.3	---
W-PROX-L	11.80 + 0.58 10.6 - 12.7	11.09 + 0.56 10.1 - 12.2	10.14 + 0.51 (5) 9.3 - 10.7	---

Table 4.10--continued.

Measurements	<i>P. a. auritus</i>	<i>P. a. floridanus</i>	<i>P. wetmorei</i>	<i>Phalacrocorax</i> sp.
W-DIST-CR	11.64 ± 0.36 11.1 - 12.3	11.06 ± 0.50 10.2 - 11.9	11.57 ± 0.49 (25) 10.6 - 12.4	11.1; 10.6
W-DIST-CD	11.16 ± 0.40 10.3 - 11.6	10.47 ± 0.50 9.8 - 11.6	11.04 ± 0.60 (21) 9.8 - 12.0	10.7
D-MCON	10.98 ± 0.42 10.5 - 11.6	10.41 ± 0.60 9.2 - 12.0	11.59 ± 0.40 (38) 10.5 - 12.3	10.6
D-LCON	10.15 ± 0.28 9.8 - 10.7	9.76 ± 0.45 9.0 - 10.7	10.14 ± 0.35 (31) 9.6 - 10.8	9.4
D-ICON	6.31 ± 0.44 5.4 - 6.7	5.70 ± 0.34 5.1 - 6.4	6.43 ± 0.26 (40) 6.1 - 7.0	6.1; 6.0

Table 4.11. Measurements of the tarsometatarsi of the cormorants *Phalacrocorax auritus auritus* ($N = 14$, 7 males, 7 females), *Phalacrocorax auritus floridanus* ($N = 18$, 9 males, 9 females), and *Phalacrocorax vetmorei*, from the Bone Valley Mining District, and Phalacrocorax species from the Love Bone Bed and McGehee Farm local faunas. Data are mean \pm standard deviation, (N), and range. Abbreviations are defined in the methods section.

Measurements	P. a. auritus	P. a. floridanus	P. wetmorei	McGehee Farm	Love
Tarsometatarsus					
LENGTH	62.01 ± 2.42 $55.2 - 65.0$	59.50 ± 2.41 $54.7 - 63.6$	61.62 ± 3.68 (5) $60.3 - 69.2$	57.7	—
W-SHAFT	5.94 ± 0.37 $5.3 - 6.6$	5.83 ± 0.14 $5.1 - 6.9$	6.17 ± 0.38 (13) $5.8 - 7.0$	5.5; 6.2	—
D-SHAFT	5.24 ± 0.24 $4.9 - 5.6$	5.27 ± 0.52 $4.6 - 6.2$	5.53 ± 0.44 (13) $4.9 - 6.2$	5.1; 5.1	—
W-PROX	12.84 ± 0.44 $12.0 - 13.6$	12.20 ± 0.57 $11.0 - 13.4$	12.96 ± 0.47 (22) $12.1 - 14.1$	11.5; 11.7	—
D-MCOT	8.70 ± 0.38 $8.0 - 9.2$	8.44 ± 0.29 $7.9 - 9.0$	9.01 ± 0.58 (21) $8.1 - 10.0$	7.9; 8.1	—
D-LCOT	7.42 ± 0.44 $6.8 - 7.9$	7.25 ± 0.49 $6.5 - 8.3$	7.22 ± 0.42 (20) $6.6 - 8.3$	6.7; 7.2	—
W-HYPOIS	5.61 ± 0.21 $5.3 - 6.0$	5.52 ± 0.27 $5.0 - 5.9$	6.38 ± 0.65 (9) $5.6 - 7.8$	5.5; 6.1	—
L-HYPOIS	9.67 ± 0.67 $9.1 - 10.7$	9.74 ± 0.62 $9.0 - 11.0$	10.62 ± 1.02 (11) $8.7 - 12.6$	9.6; 9.7	—

Table 4.11--continued

Measurements	P. a. auritus	P. a. floridanus	P. wetmorei	McGehee Farm	Love
D-PROX-M	17.66 ± 0.54 $16.6 - 18.5$	16.90 ± 0.66 $15.5 - 18.3$	17.24 ± 0.72 (15) $16.4 - 19.0$	16.1; 16.7	—
D-D-SHAFT	4.59 ± 0.34 $4.2 - 5.3$	4.27 ± 0.26 $3.6 - 4.7$	4.54 ± 0.21 (30) $3.9 - 4.9$	4.1	4.5
W-DIST	14.64 ± 0.36 $14.0 - 15.1$	14.11 ± 0.61 $12.6 - 14.9$	14.12 ± 0.49 (25) $13.2 - 15.8$	13.6	—
W-TRII	3.94 ± 0.17 $3.7 - 4.2$	3.81 ± 0.23 $3.2 - 4.0$	4.16 ± 0.27 (18) $3.6 - 4.5$	3.9	—
D-TRII	6.20 ± 0.29 $5.7 - 6.7$	5.92 ± 0.35 $5.0 - 6.3$	6.07 ± 0.19 (20) $5.7 - 6.4$	5.6	—
W-TRIII	4.99 ± 0.21 $4.6 - 5.4$	4.78 ± 0.38 $4.0 - 5.9$	5.21 ± 0.28 (30) $4.3 - 5.8$	4.8	4.9
D-TRIII	6.89 ± 0.25 $6.5 - 7.3$	6.48 ± 0.34 $5.7 - 6.7$	6.89 ± 0.29 (29) $6.1 - 7.6?$	6.8	6.7
W-TRIV	4.02 ± 0.22 $3.6 - 4.3$	3.86 ± 0.21 $3.5 - 4.2$	4.04 ± 0.29 (23) $3.4 - 4.5$	3.6	4.3
D-TRIV	8.16 ± 0.21 $7.9 - 8.5$	7.84 ± 0.35 $7.0 - 8.4$	6.65 ± 0.27 (25) $5.9 - 7.2?$	6.2	6.4

Family Anhingidae Ridgway, 1887

Remarks. Skeletal elements of anhingas discussed below may be distinguished from the Phalacrocoracidae as follows: Humerus--by characters given by Miller (1966) and Martin and Mengel (1975). Coracoid --head rotated ventrad and mediad, to produce a distinct notch between head and shaft, when observed from either a ventral or medial view (head merges smoothly with shaft in the Phalacrocoracidae). Procoracid expanded and concave cotyla scapularis present.

Genus Anhinga Brisson, 1760

Anhinga grandis Martin and Mengel, 1975

Material. Love Bone Bed local fauna; UF 25739, proximal end right humerus; UF 25723, UF25725, distal ends right humeri; UF 26000, nearly complete right coracoid; UF 25873, distal end right tibiotarsus.

McGehee Farm local fauna; UF 11107, distal end right humerus.

Remarks. Elements described in detail in Becker (in prep.). Distal humeri compare exactly in all features with the type. Coracoid assigned to this species, as it is of correct size.

Anhinga sp. unknown

Material. Bone Valley Mining District, no specific locality; UF 29781, proximal end left ulna; UF 29780, distal end left ulna.

Remarks. The ulnae are much larger than comparable elements of A. anhinga and those expected for A. grandis. Parenthetically, the ulna from Coleman III (UF 16664), referred to A. cf. grandis by Ritchie (1980), is definitely not Anhinga grandis and is not identifiable to a species. Along with the two specimens from Bone Valley, this Coleman III specimen represents a much larger species of anhinga which existed approximately

4.5 million years later than did A. grandis. Unfortunately, this species is only known from ulnae and not from more diagnostic elements.

Remarks on the Family Anhingidae.

The earliest record of the Anhingidae is Protoplotus beauforti Lambrecht based on a skeletal impression, from the late Eocene of Sumatra. It is presently being restudied and will probably be referred to a new family (P. V. Rich--in litt., cited in Olson, ms.).

Anhinga pannonica Lambrecht was described from a cervical vertebra and carpometacarpus from the late Miocene of Tataros, Hungary. Rich (1972) also assigned another cervical vertebra and a partial humerus from the late Miocene of Tunisia to this species. The only other anhinga known from the late Miocene, Anhinga grandis, originally described from the Hemphillian Cambridge (Ft.- 40) locality, Nebraska, is discussed above.

The validity of A. laticeps Devis from the late Pleistocene of Australia is somewhat questionable (Brodkorb and Mourer-Chauvire, 1982; Olson, ms.). Anhinga hadarensis Brodkorb and Mourer-Chauvire, 1982 from the Upper Pliocene Kadar Hadar member of the Hadar Formation, Ethiopia is also known from the Omo Basin, Ethiopia, and Olduvai Gorge, Tanzania. It appears to be the immediate ancestor to A. rufa (Brodkorb and Mourer-Chauvire, 1982). Two Pleistocene fossil species of anhingas have been shown to be cormorants. Anhinga parva Devis from Australia was shown by Miller (1966) to be the cormorant Phalacrocorax melanoleucus and A. nana Newton and Gadow, from Mauritius was shown by Olson (1975a) to be another cormorant, Phalacrocorax africanus.

Order Ciconiiformes Garrod, 1874 (Auct.)Family Ardeidae Vigors, 1825.

Remarks. The following account briefly establishes the presence and distribution of the late Miocene and early Pliocene herons in Florida for the paleoecological and biochronological aspects of this study. More detailed descriptions and systematic remarks may be found in Becker (1985a). Systematic nomenclature follows Payne and Risley (1976).

Genus Ardea Linnaeus, 1758Ardea polkensis Brodkorb, 1955

Material. Bone Valley Phosphate Mining District, Palmetto Mine; PB 380, proximal end of right tarsometatarsus (type), UF 21138, distal end right tarsometatarsus; Payne Creek Mine; PB 7924, humeral end of right coracoid.

Remarks. This heron is about the size of A. cinerea and is a rare member of the Bone Valley avifauna. On the material now known for this species, it is not possible to determine its relationship to other members of the genus Ardea.

Ardea sp. indet.

Material. Love Bone Bed local fauna; UF 25939, distal end left tarsometatarsus, missing trochlea IV.

Remarks. This specimen represents a species of Ardea about the size of A. herodias occidentalis.

Genus Egretta T. Forster, 1817Egretta subfluvia Becker, 1985

Material. Withlacoochee River 4A local fauna; UF 19001, right tarsometatarsus lacking only trochlea IV and hypotarsus.

Remarks. This species is a small heron about the size of Egretta

ibis, and is only known from the holotype. The tarsometatarsus is proportionally narrower than in other members of this genus.

Egretta sp. indet.

Material. Love Bone Bed local fauna; UF 25759, proximal end of left carpometacarpus, UF 26082, distal end right ulna. Bone Valley Phosphate Mining District, Payne Creek Mine; PB 7925, coracoid.

Remarks. These specimens fall within the size range of the living E. rufescens. Because of the large time interval (4.5 MA) between the Love Bone Bed and the Bone Valley, it is unlikely that these elements represent the same species.

Genus Ardeola Boie, 1822

Ardeola sp. indet.

Material. Love Bone Bed local fauna; UF 25940, distal one-third left tarsometatarsus.

Remarks. Small, similar in size to Ardeola striata. Taxonomic assignment based entirely on size.

Subfamily Nycticoracinae Payne and Risley, 1976

Genus Nycticorax T. Forster, 1817

Nycticorax fidens Brodkorb, 1963

Material. McGehee Farm local fauna; UF 3285, complete left femur.

Remarks. See Brodkorb (1963a) for description and remarks.

Remarks on the Family Ardeidae.

Table 4.1 summarizes the distribution of the fossil herons from Florida. The Love Bone Bed local fauna has produced three herons--a small Ardeola, a large Egretta, and a very large Ardea. It is most

probable that these fossil herons were members of the same diurnal fish-eating guild as are their modern counterparts. It is not surprising that three herons occur together. As many as 12 species of herons occur sympatrically in Florida today. They coexist by partitioning resources such as size and kind of prey, use of habitat (e.g. water depth), and foraging behavior (Recher and Recher, 1980).

The two herons from Bone Valley could possibly be viewed as marine specialists--one medium-sized specializing on small prey and the other specializing on larger prey, as the living Egretta rufescens and Ardea herodias occidentalis do today.

Little can be said of the paleoecology of Egretta sp. from the Withlacoochee River 4A but perhaps it was similar to E. ibis in its ecology, as it is similar to this species in its morphology.

Family Ciconiidae (Gray, 1840)

Remarks. There are only a few characters on the skeletal elements preserved here that can distinguish between the genera Mycteria, Ciconia, and Jabiru (sensu Kahl, 1972). Size is of no generic value as evidenced by species of Ciconia overlapping with species of all other ciconiid genera.

Characters on the distal end of the tibiotarsus include the internal ligamental prominence (= medial epicondyle) well-developed in Jabiru (less so in Mycteria and Ciconia); distal end laterally compressed in Mycteria (less so in Ciconia, except the atypical C. abdimii and C. episcopus; somewhat compressed in Jabiru); distal opening of the tendinal canal more medially placed in Jabiru than in Ciconia or Mycteria; tubercle slightly elevated above the surface of a strong ridge connecting

the lateral condyle and tubercle in Mycteria (much more elevated in Jabiru and Ciconia, excluding C. abdimii and episcopus). Proximal tarsometatarsus with sulcus ligamentosus sloping gently to the hypotarsus in Mycteria (sharply sloping and usually deeply excavated in Ciconia and Jabiru). Tibiotarsi and tarsometatarsi of all species of ciconiids (14 species total) were examined except those of Ciconia nigra, Ephippiorhynchus senegalensis, and Leptoptilos crumeniferus.

Subfamily Mycteriinae American Ornithologists' Union, 1908

Genus Mycteria Linnaeus, 1758

Mycteria sp. A

Material. Love Bone Bed local fauna; UF 25990, proximal end right tarsometatarsus (questionably referred).

McGehee Farm local fauna: UF 29475, proximal end right tarsometatarsus.

Description. UF 25990 with hypotarsus broken. Tentatively referred to Mycteria by having the intercotylar prominence sharp and elevated, as in modern species of Mycteria (prominence more rounded in Ciconia and Jabiru). UF 29475 agrees with Mycteria by having the intercotylar prominence highly raised and the sulcus ligamentosus sloping gradually toward the hypotarsus (sharply notched in Ciconia). There are no qualitative characters outside the range of variation of the modern species Mycteria americana, except possibly having the hypotarsus slightly lower on the shaft.

Remarks. As Table 4.12 shows, this fossil material is within the range of a modern population of Mycteria americana. However, the proportions are slightly different, with the proximal tarsometatarsus

proportionally slightly wider than expected (Figure 4.1). It is very likely that this material represents a species separate from the living one. Mycteria wetmorei Howard, 1935, from the Pleistocene of California, was described on the basis of a lower mandible and is said to be larger than the living Mycteria americana. As there is unstudied post-cranial material of this fossil species in many U. S. museum collections, this material should be examined and Mycteria wetmorei revised before determining the exact systematic position of the fossil material from Florida.

Subfamily Ciconiinae Gray, 1840

Genus Ciconia Brisson, 1760

Ciconia sp. A.

Material. Love Bone Bed local fauna; UF 26102, UF 29674, distal ends left tibiotarsi; UF 25906, UF 25909, distal ends right tibiotarsi; UF 25946, distal end left tarsometatarsus. UF 29675, distal shaft right tibiotarsus; UF 25900, distal end left tibiotarsus (tentatively referred).

Description. Size similar to that of Ciconia ciconia. Distal end of tibiotarsus agrees with those of Ciconia by having the anterior intercondylar sulcus broad (narrow in Mycteria) and the distal end not laterally compressed (laterally compressed in Mycteria). Process for the ligamental attachment above the distal end of the external condyle is intermediate between papilla-like (as in Jabiru) and crest-like (as in Ciconia). See Figure 4.2 for comparisons with other species of Ciconia.

Distal end of tarsometatarsus agrees with Ciconia in having trochlea II less rotated ventrally (Mycteria more ventrally rotated). UF 29675

and UF 25900 are referred here strictly on the basis of size. Both are too broken and/or worn for further description.

Remarks. See remarks pertaining to Ciconia sp. B., below.

Ciconia sp. B.

Material. Mixson's Bone Bed; F:AM 120-2185, distal end right tibiotarsus; F:AM 205-3008, distal end left tibiotarsus. Bone Valley Mining District, Palmetto Mine; UF 21135, distal end right tibiotarsus; UF 21063, distal end left tarsometatarsus missing trochlea IV (tentatively referred).

Description. Distal tibiotarsus (F:AM 120-2195) larger than that of C. marguari, similar in size to that of a small Jabiru. Agrees with Ciconia by having the process for the ligamentous attachment above the distal end of the external condyle ridge-like (papilla-like in Jabiru), and by having the distal opening of the tendinal canal placed more toward the edge of the bone (more toward the middle of the bone in Jabiru). Agrees with Jabiru in having the distal end slightly laterally compressed.

Distal tibiotarsus (UF 21135) similar to F:AM 120-2185, but with a robust shaft and having the distal opening of the tendinal canal more toward the middle of the bone. Very similar to some specimens of Jabiru, but can be distinguished from this genus by having the ridge from the condyle to tubercle slightly notched, and the ligamentous attachment above the distal end of the external condyle ridge-like (as in Ciconia). See Figure 4.2 for comparisons with other species of Ciconia.

Tarsometatarsus fragment assigned on size.

Remarks. The presence of this species, species A. above, and species C. below, shows that the genus Ciconia was much more diverse in North America than was previously known.

cf. Ciconia sp. C

Material. Bone Valley Mining District, Swift Mine (=Estech); UF 52958, distal end left tibiotarsus. Palmetto Mine; UF 12470, distal end left tarsometatarsus missing trochlea IV (tentatively referred).

Description. Distal end of tibiotarsus (UF 52958) extremely large, in the size range of Jabiru mycteria. Distal end slightly laterally compressed (as in Jabiru). As in Ciconia, the external ligamental attachment is ridge-like and distal opening of tendinal bridge is toward the edge of the bone (*contra Jabiru*). See Figure 4.2 for comparisons with other species of Ciconia.

Tarsometatarsus assigned here on the basis of size.

Remarks. Although referable to the genus Ciconia on the basis of the above characters, this specimen bears a striking resemblance to that of Jabiru mycteria. Were it not for Howard's (1942) study of Ciconia maltha and Jabiru mycteria, I would be tempted to suggest that C. maltha and J. mycteria are congeneric. Ciconia sp. C. is probably closely related to the clade which gave rise to Ciconia maltha.

Remarks on the Family Ciconiidae.

Living species of storks have been revised by Kahl (1971, 1972) who synonymized a number of monotypic genera in Peters (1931). Wood (1983, 1984) has analyzed the phenetic relationships within the Ciconiidae. Apart from the substantial criticisms which have been made on the use of phenetics as a basis for classifications (Mayr, 1969; Hull, 1970;

Johnson, 1970) I would also note that Wood used an extremely small sample size (2 - 6 individuals per species, many of which were unsexed), which prevented him from adequately accounting for the considerable sexual variation which exists in storks.

The fossil species of storks are in critical need of revision. All fossil species now known were described before Kahl's revisions (1971, 1972) which reduced the number of recent genera from 11 to 6. Because of the plethora of monotypic genera in this family at the time of the description of the fossil species, workers have tended to underestimate the amount of morphological differences within a single genus (*sensu* Kahl). Because of this, it is now often impossible to determine relationships between fossil and recent genera.

A number of species originally described as storks have since been moved to other families or synonymized with other species, or both. These include Pelargopappus stehlini and P. trouessartii (= Amphiperentarius schlosseri; Chauvire, in litt., to Olson, ms), Amphipelargus majori (Ergilornithidae; Harrison, 1981), Palaeopelargus nobilis, Xenorhynchopsis tibialis, X. minor, and Xenorhynchus nanus (2 are flamingos, Rich, 1976; 2 in need of restudy, Olson, ms), and Ibis milne-edwardsi (= Miophasianus altus; Olson, 1974b). Lists of the other fossil storks may be found in Brodkorb (1963c). Most of these are in need of restudy.

In North America, fossil species of storks include Propelargus olsoni Brodkorb from the Seaboard Airline Railroad local fauna in Tallahassee of Barstovian age (see comments on the generic status of Propelargus in Olson, ms), Ciconia maltha Miller now known from the Blancan through the Rancholabrean of Idaho, California, and Florida, and

Mycteria wetmorei Howard from the Rancholabrean of California and Florida. These species are also poorly defined on their postcranial skeleton and are in need of revision.

The fossil species of storks in the late Miocene and early Pliocene of Florida show Mycteria to be long established (Clarendonian to Recent) and Ciconia to be more diverse in the past. The relationships between Ciconia maltha, Ciconia sp. C., and Jabiru mycteria should be further investigated.

Figure 4.1. Plot of the transverse width of the proximal end (W-PROX) versus depth of medial cotoyla (D-MCOT) of the tarsometatarsi of the Recent *Mycteria americana* and *Mycteria* sp. A from the Love Bone Bed (L) and the McGhee Farm (M) local faunas. Sex of Recent individuals is indicated by an arrow (male) or cross (female) on the symbols.

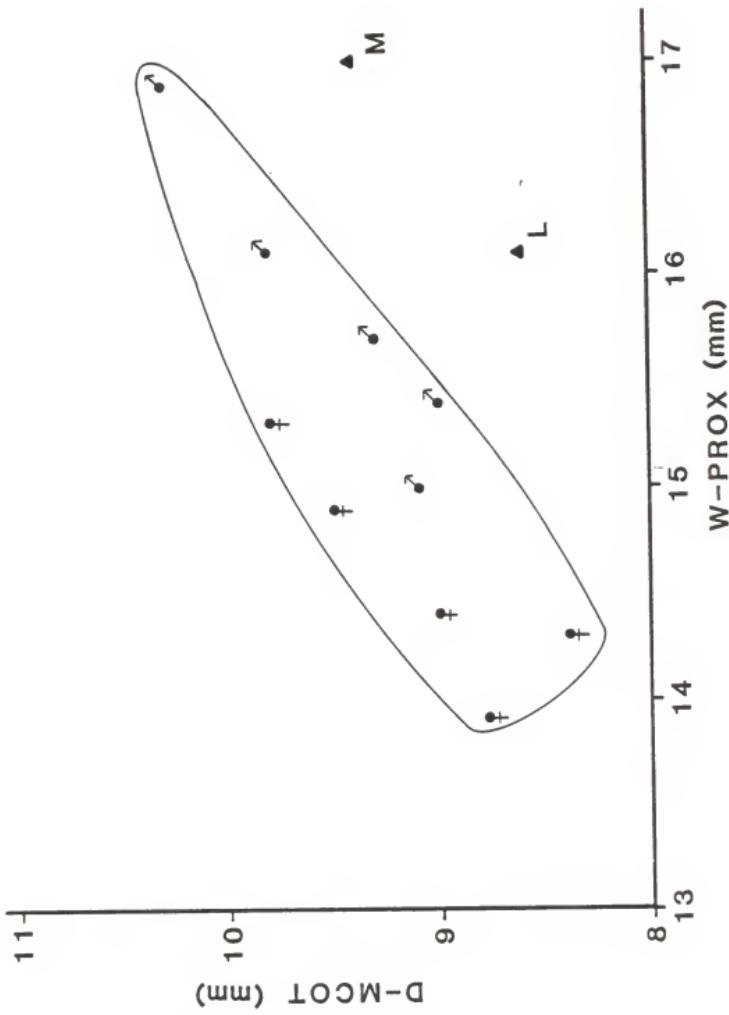


Figure 4.2. Plot of transverse width of the distal end, across the cranial surface (W-DIST-CR) versus the depth of the area intercondylaris (D-ICON) of the tibiotarsi of the following ciconiid species: (1) Ciconia abdimii, (2) C. episcopus, (3) C. nigra, (4) C. ciconia, (5) C. maguari, (6) C. maltha from the Pleistocene of Florida, (7) Jabiru mycteria, (triangles) Ciconia sp. A from the Love Bone Bed, (squares) Ciconia sp. B from the Mixson and Bone Valley local faunas, and (open circle) Ciconia sp. C from the Bone Valley local fauna.

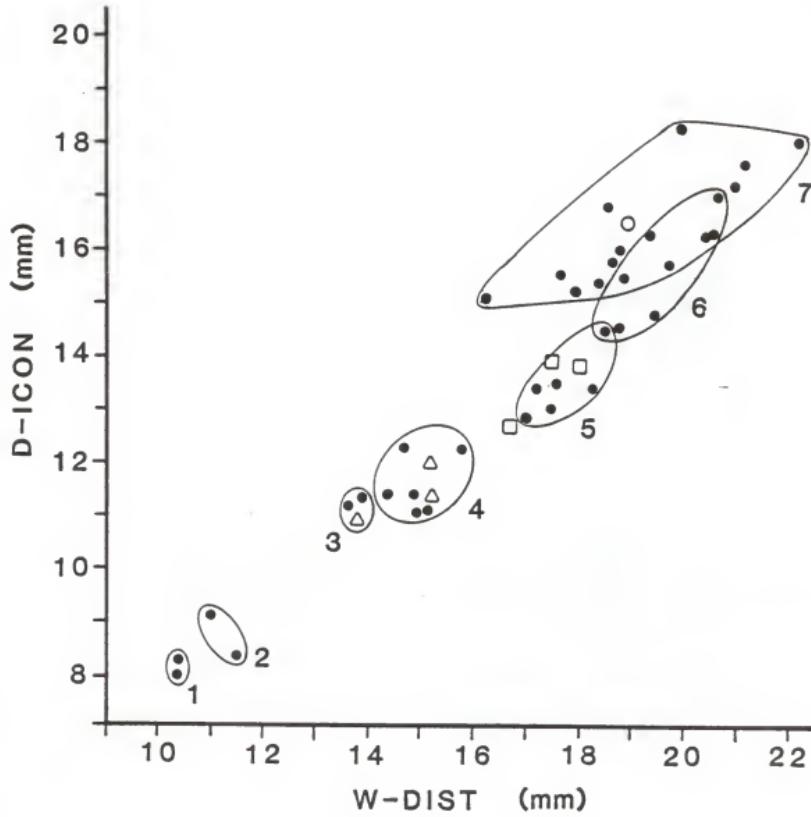


Table 4.12. Measurements of the tarsometatarsi of the storks Mycteria americana (N = 10, 5 males, 5 females) and Mycteria species A. from the Love Bone Bed and the McGehee Farm local fauna. Data are mean \pm standard deviation and range. Abbreviations are defined in the methods section.
 (*) Specimen broken.

<u>Measurements</u>	<u>Mycteria americana</u>	<u>Mycteria</u> sp. A
Tarsometatarsus		
W-PROX	15.19 \pm 0.90 13.9 - 16.9	17.0; 16.1
D-MCOT	9.30 \pm 0.56 8.4 - 10.3	9.4; 8.6
D-LCOT	8.88 \pm 0.60 8.1 - 9.8	9.6; 9.5*
W-HYPOTS	9.66 \pm 0.62 8.5 - 10.5	9.5
D-PROX-L	16.57 \pm 0.94 15.3 - 17.8	17.2

Table 4.13. Measurements of the tibiotarsi of the Recent storks *Jabiru mycteria* (N= 13, 2 males, 5 females, 6 unsexed), *Ciconia maguari* (N = 5, 1 male, 1 female, 3 unsexed), and *Ciconia ciconia* (N= 6, 2 males, 4 unsexed). Data are mean \pm standard deviation and range. Abbreviations are defined in the methods section.

<u>Measurement</u>	<u><i>Ciconia ciconia</i></u>	<u><i>Ciconia maguari</i></u>	<u><i>Jabiru mycteria</i></u>
Tibiotarsus			
W-SHAFT	8.38 \pm 0.56 7.6 - 9.0	9.50 \pm 0.48 8.8 - 10.0	11.13 \pm 0.91 9.6 - 12.7
D-SHAFT	7.22 \pm 0.48 6.6 - 7.7	8.26 \pm 0.30 7.8 - 8.6	10.37 \pm 0.64 9.3 - 11.1
W-DIST-CR	14.98 \pm 0.47 14.4 - 15.8	17.72 \pm 0.66 17.0 - 18.5	19.21 \pm 1.58 16.3 - 22.3
W-DIST-CD	11.87 \pm 0.95 10.7 - 13.0	14.56 \pm 0.35 14.0 - 14.9	16.35 \pm 1.31 13.6 - 18.9
D-MCON	18.97 \pm 1.13 17.9 - 20.4	21.46 \pm 0.95 20.6 - 22.8	25.78 \pm 1.76 23.4 - 28.7
D-LCON	18.65 \pm 0.55 18.4 - 19.3	21.14 \pm 0.69 20.4 - 22.1	24.37 \pm 1.68 22.2 - 27.4
D-ICON	11.60 \pm 0.56 11.1 - 12.3	13.52 \pm 0.61 12.8 - 14.5	16.31 \pm 1.07 15.1 - 18.3

Table 4.14. Measurements of the tibiotarsi of the fossil storks from Florida; Ciconia sp. A, from the Love Bone Bed Local fauna, Ciconia sp. B, from the Bone Valley Mining District and Mixson local fauna, Ciconia sp. C, from the Bone Valley Mining District, and Ciconia maltha from various Pleistocene localities in Florida. Data are mean + standard deviation and range. Abbreviations are defined in the methods section. Compare measurements with those in Table 4.13.

Measurements	<u>Ciconia</u> sp. A	<u>Ciconia</u> sp. B	<u>Ciconia</u> sp. C	<u>Ciconia</u> maltha
Tibiotarsus				
W-SHAFT	9.04 + 0.66 (5) 8.1 - 9.6	9.8; 10.2; 11.8*	12.3	12.60 + 1.09 (6) 11.7 - 12.7
D-SHAFT	7.80 + 0.53 (5) 7.1 - 8.5	8.4; 8.3; 9.1	11.3	10.01 + 0.75 (7) 9.0 - 11.1
W-DIST-CR	14.23 + 0.84 (3) 13.7 - 15.2	17.5; 16.6; 18.0	19.1	19.47 + 0.90 (6) 18.5 - 20.6
W-DIST-CD	*11.5	14.2; 13.7; 13.2	15.0	15.98 + 0.68 (5) 15.3 - 17.0
D-MCON	18.5; 18.9	22.8; 21.7; 22.5	26.4	24.80 + 1.57 (5) 22.9 - 26.9
D-LCON	18.8; 18.9	22.6; 20.8; 22.4	25.5	24.62 + 1.67 (5) 23.0 - 26.7
D-ICON	11.48 + 0.28 (5) 11.2 - 11.9	13.9; 13.0; 13.8	16.5	15.51 + 0.99 (7) 14.5 - 17.1

Family Plataleidae Bonaparte, 1838

Subfamily Threskiornithinae (Richmond, 1917)

Genus Eudocimus Wagler, 1832Eudocimus sp. A

Material. Bone Valley Mining District, Gardinier Mine; UF 60040, distal end left tibiotarsus. Palmetto Mine, PB 7749, proximal end left tarsometatarsus.

Description. Tibiotarsus similar in size and general morphology to large individuals (males) of Eudocimus albus or E. ruber. Tendinal bridge as in E. ruber (shorter in E. albus), tubercle well-developed (as in E. albus, less developed in E. ruber), extensor sulcus more excavated and flattened than either E. ruber or E. albus, well-developed crest curves obliquely toward lateral face from tubercle (crest well developed and oriented parallel to the long axis of the shaft in both E. albus and E. ruber). Lateral margins of lateral condyle not as developed as in E. albus or E. ruber. Proximal border of the posterior articular surface extends farther proximally on the external side of the fossil (border is usually straight in E. albus and E. ruber; this condition similar in some individuals of Plegadis spp., especially P. ridgwayi).

Tarsometatarsus similar in size and overall morphology to Eudocimus albus and E. ruber. I can find no character on the fossil specimen that is not within the range of variation of these two species.

Remarks. Olson (1981b), in his review of the fossil ibises reported Eudocimus sp. from a distal end of a tarsometatarsus from Bone Valley. I have not been able to locate a distal tarsometatarsus in either the Brodkorb collection or in the FSM collections. I therefore conclude that

Olson erroneously reported PB 7749 as a distal end rather than a proximal end.

Nothing prevents the two specimens listed above from representing the same species. Despite the apparent difference in size, the Bone Valley specimens (see Table 4.15) and USNM 181027 from Lee Creek could easily represent the same species of Eudocimus. The geologic ages are similar, both fall within the size variation of a single species (see Figure 4.3, where both specimens fall within the size range of E. albus), and both USNM 181027 and UF 60040 have the proximal border of the posterior articular surface extending farther proximally on the external side. The distribution of this last character in some specimens of Plegadis species cannot be evaluated with the skeletal material presently available.

Genus Plegadis Kaup, 1829

Plegadis cf. P. pharangites (A. H. Miller and Bowman, 1956)

Material. Love Bone Bed local fauna; UF 25870, distal end right tibiotarsus.

Description. Tibiotarsus similar in size to a very small Plegadis chihi or P. ridgwayi. Distinguished from these species by having a more distinct tuberculum on the distal end, a more gracile shaft, lateral condyle merging with the shaft less abruptly, and the surface cranial to the tendinal bridge more excavated.

Remarks. The material from the Love Bone Bed is not directly comparable to that of Plegadis pharangites. Skeletal elements of both P. pharangites and P. cf. P. pharangites are approximately 10 to 12 percent smaller than P. mexicana (=P. chihi). While I doubt that this material from the late Clarendonian of Florida is conspecific with that from the

Blancan of Texas, I cannot demonstrate any qualitative differences and have therefore referred this distal end of a tibiotarsus to P. pharangites strictly on the basis of size.

Threskiornithinae, gen. et sp. indet.

Material. Love Bone Bed local fauna; UF 26003, humeral end right coracoid.

Description. Humeral end coracoid with ventral portion of head abraded and with procoracoid broken and missing. Size of a large Plegadis falcinellus, but also within the range of Eudocimus albus or E. ruber. The impression for the acrocoracohumeralis ligament is wider in the fossil specimen than in either Plegadis or Eudocimus. In anterior view, the shaft appears wider, resembling Eudocimus rather than Plegadis.

Remarks. I can find no consistent characters on the humeral end of the coracoid which will discriminate with confidence between species of Plegadis and Eudocimus. This specimen is probably too large to represent the other ibis (Plegadis cf. P. pharangites) from the Love Bone Bed.

Remarks on the Family Plateleidae.

Olson (1981b) has recently discussed the fossil record of ibises. There has been no additional species described since the appearance of his paper.

I have not been able to find consistent osteological characters which can separate all specimens of Eudocimus ruber from E. albus. Considering that most skeletal measurements of these two species overlap extensively (compare in Table 4.15), and that these "species" interbred freely when E. ruber was introduced into south Florida, these two taxa should probably be regarded as two color morphs of the same species. As

Olson (1981b) notes, doing this would cast considerable doubt on the validity of Eudocimus peruvianus Campbell. Campbell (1979) states that E. ruber differs more from E. albus and E. peruvianus than the latter two do from each other. It is very likely that when a larger series of recent E. ruber and E. albus are examined and compared with E. peruvianus, there will be no consistent osteological differences between these three species.

Similarly, Plegadis falcinellus and P. chihi are very similar osteologically and may possibly be conspecific (see Table 4.16 for measurements; Palmer, 1962; Mayr and Short, 1970 for comments).

Figure 4.3. Plot of transverse width of distal end across the caudal surface (W-DIST-CD) versus depth of medial condyle (D-MCON) of the tibiotarsi of the following species of ibis: (1) Eudocimus albus, (2) E. ruber, (3) Plegadis falcinellus, (4) P. chihi, (5) P. ridgwayi, (A) Eudocimus sp. from the Lee Creek l. f., (B) Eudocimus sp. A from the Bone Valley l. f., and (C) Plegadis cf. P. pharangites from the Love Bone Bed local fauna.

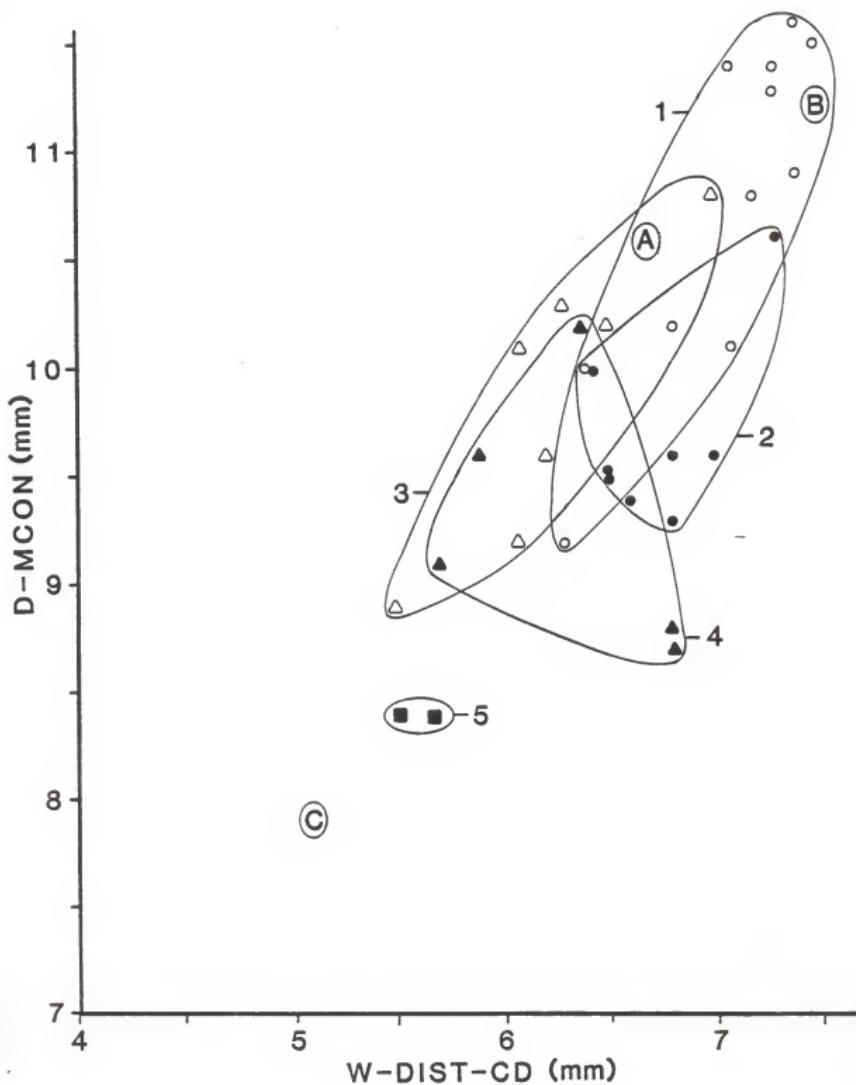


Table 4.15. Measurements of tibiotarsi, coracoids, and tarsometatarsi of the ibises *Eudocimus ruber* ($N = 8$, 2 males, 6 females), *Eudocimus albus* ($N = 12$, 6 males, 6 females), and *Eudocimus* species from the Bone Valley Mining District. Data are mean \pm standard deviation and range. Abbreviations are defined in the methods section.

<u>Measurements</u>	<u><i>Eudocimus ruber</i></u>	<u><i>Eudocimus albus</i></u>	<u><i>Eudocimus</i> sp.</u>
Tibiotarsus			
W-SHAFT	4.90 ± 0.20 $4.7 - 5.3$	5.02 ± 0.40 $4.5 - 5.6$	5.6
D-SHAFT	4.09 ± 0.20 $3.8 - 4.5$	4.53 ± 0.53 $3.9 - 5.8$	4.7
W-DIST-CR	9.09 ± 0.64 $8.5 - 10.5$	9.74 ± 0.74 $8.5 - 10.5$	10.7
W-DIST CD	6.74 ± 0.30 $6.4 - 7.3$	7.07 ± 0.41 $6.3 - 7.5$	7.5
D-MCON	9.69 ± 0.42 $9.3 - 10.6$	10.76 ± 0.78 $9.2 - 11.6$	11.2
D-LCON	9.14 ± 0.50 $8.6 - 10.2$	10.26 ± 0.69 $9.1 - 11.1$	10.8
D-ICON	6.04 ± 0.27 $5.8 - 6.6$	6.70 ± 0.60 $5.7 - 7.3$	6.9
-			

Table 4.15--continued

<u>Measurements</u>	<u><i>Eudocimus ruber</i></u>	<u><i>Eudocimus albus</i></u>	<u><i>Eudocimus sp.</i></u>
Coracoid			
HEAD-CS	14.46 \pm 0.51 13.7 - 15.1	15.52 \pm 1.02 13.4 - 17.0	--
W-SHAFT	5.51 \pm 0.31 5.2 - 6.1	5.93 \pm 0.41 5.0 - 6.5	--
D-SHAFT	4.84 \pm 0.32 4.4 - 5.4	5.04 \pm 0.33 4.4 - 5.4	--
L-GLEN	9.50 \pm 0.35 8.9 - 9.9	10.50 \pm 0.44 9.8 - 11.1	--
Tarsometatarsus			
W-PROX	10.76 \pm 0.83 10.1 - 12.6	11.47 \pm 0.98 10.2 - 12.8	10.3
D-MCOT	5.03 \pm 0.27 4.7 - 5.4	5.47 \pm 0.37 4.7 5.9	5.0
W-HYPOTS	5.24 \pm 0.37 4.8 - 5.8	5.65 \pm 0.54 4.9 - 6.5	5.5
D-PROX-L	9.33 \pm 0.49 8.8 - 10.4	10.33 \pm 0.73 9.1 - 11.3	9.5

Table 4.16. Measurements of tibiotarsi, coracoids, and tarsometatarsi of the ibises Plegadis ridgwayi ($N = 2$, unsexed), Plegadis chihi ($N = 7$, 2 males, 2 females, 3 unsexed; number may be less due to incomplete specimens), Plegadis falcinellus ($N = 10$, 7 males, 3 females), Plegadis species (tibiotarsus) and Threskiornithinae, genus and species indet. (coracoid) from the Love Bone Bed local fauna. Data are mean + standard deviation and range. Abbreviations are defined in the methods section. (*) specimen damaged.

<u>Measurements</u>	<u>P. ridgwayi</u>	<u>P. chihi</u>	<u>P. falcineillus</u>	<u>Plegadis</u> sp.
Tibiotarsus				
W-SHAFT	4.0; 4.3	4.33 + 0.47 3.8 - 4.9	4.52 + 0.37 3.9 - 5.0	3.7
D-SHAFT	3.4; 3.6	3.80 + 0.35 3.5 - 4.3	4.05 + 0.34 3.6 - 4.7	3.2
W-DIST-CR	7.5; 7.9	8.45 + 0.66 7.6 - 9.1	8.63 + 0.56 7.8 - 9.7	7.2
W-DIST-CD	5.7; 5.5	5.93 + 0.32 5.7 - 6.4	6.28 + 0.43 5.5 - 7.0	*5.1
D-MCON	8.4; 8.4	9.20 + 0.69 8.7 - 10.2	9.93 + 0.58 8.9 - 10.8	*7.9
D-LCON	8.1; 8.3	9.18 + 0.75 8.3 - 10.1	9.56 + 0.71 8.5 - 10.5	*7.1
D-ICON	5.6; 5.5	6.34 + 0.54 5.8 - 7.0	6.39 + 0.43 5.8 - 7.0	4.9

Table 4.16--continued

<u>Measurements</u>	<u>P. ridgwayi</u>	<u>P. chihhi</u>	<u>P. falcinellus</u>	<u>Threskiornithinae</u> <u>gen. et sp. indet.</u>
Coracoid HEAD-CS	12.6; 12.7	13.42 ± 0.78 12.3 - 14.3	13.99 ± 0.86 12.2 - 15.0	16.2
W-SHAFT ^W	5.4; 5.4	5.37 ± 0.50 4.6 - 5.9	5.52 ± 0.54 4.6 - 6.3	6.1
D-SHAFT ^D	3.7; 4.0	4.45 ± 0.38 3.9 - 4.9	4.54 ± 0.38 4.0 - 5.1	5.0
L-GLEN	8.5; 9.0	8.97 ± 0.33 8.5 - 9.4	9.54 ± 0.69 8.1 - 10.3	11.4

Order Accipitriformes (Vieillott, 1816) (Auct.)Family Vulturidae (Illiger, 1811)

Remarks. Vulture tarsometatarsi and tibiotarsi, the only elements considered here, are characterized by Cracraft and Rich (1972).

Genus *Pliogyps* Tordoff, 1959

Emended Generic Diagnosis. The tarsometatarsus of *Pliogyps* differs from that of other living and fossil genera of vultures in having a proportionally large trochlea for digit III, the proximal articular surface wide and deep in comparison to the length of the bone, a generally columnar form, with symmetrical lateral and medial flaring both proximally and distally; shaft wide in comparison to length of bone; hypotarsus merging distally with shaft by means of a broad, rounded ridge (as in *Vultur*, *Breagyps*, *Gymnogyps*, and *Geranogyps*; narrow in *Coragyps*, *Cathartes*, and *Sarcoramphus*). This last character may be strictly size dependent and if so, not of value as a generic character.

Remarks. Two other proposed generic characters (Tordoff, 1959) appear to be variable within a species, and are of no generic value. They are the shaft less deeply and extensively excavated anteriorly and groove of trochlea for digit III ending anterioproximally in a shallow, but distinct pit.

Pliogyps species

Referred Material. Love Bone Bed local fauna; UF 25719, fragment of shaft of left humerus; UF 25886, distal end left tibiotarsus; UF 25952, complete right tarsometatarsus missing a small portion of hypotarsus.

Diagnosis. Tarsometatarsus relatively more robust than any living or fossil genus of vulturid except *Pliogyps*. Tarsometatarsus distinguished from *Pliogyps fisheri* Tordoff 1959 by smaller size, by having a narrow ridge extending from the hypotarsus farther down shaft

(caudal view), by having the sulcus extensorius more excavated and extending farther down shaft (cranial view), and by having the shaft and trochlea III proportionally less deep. Pliogyps sp. from the Love Bone Bed has a proportionally greater power-arm ratio (defined below) than P. fisheri.

Description. Tarsometatarsus proportionally different from all other vultures except for Pliogyps fisheri (see Figures 4.4 - 4.6). The proximal end wide and deep. In cranial view, the proximal vascular foramina large and approximately equal in size. Papilla for the attachment of *M. tibialis cranialis* large, rounded, and in two parts. Sulcus extensoris extending down the shaft to distal foramen, with a sharp lateral border. Distinct intermuscular line extending obliquely through this sulcus (separating attachments for the extensor digitorum brevis pars hallucis and extensor digitorum brevis pars adductor-extensor digiti IV; Jollie 1976-1977:243). In caudal view, the tarsometatarsus has a long ridge extending down the shaft from the hypotarsus, terminating in an intermuscular line which then extends to the level of the articular facet of metatarsal I. See Table 4.17 for measurements.

Distal end of tibiotarsus with a broad extensor sulcus. Slight projection of bone on lateral surface (approximately 4 cm from distal end) for attachment of the fibula. Intercondylar sulcus broad; with external condyle merging evenly into it. In distal end view, the intercondylar sulcus is not symmetrical, with the lateral border sloping gradually, and the medial border sloping abruptly, up from the base of the intercondylar sulcus (symmetrical or U-shaped in Coragyps, Sarcoramphus, Breagyps, Gymnogyps; unsymmetrical or Pliogyps-like in Cathartes). See Table 4.17 for measurements.

Humerus fragment tentatively referred.

Remarks. Table 4.18 lists indices for flexion of the intertarsal joint (power-arm ratio of Jollie, 1976-1977; [(FLEXOR + LENGTH) X 100] and for robustness of shaft [W-SHAFT + LENGTH] X 100]. These indices show that Pliogyps sp. from the Love Bone Bed has an average flexion ratio but a very broad tarsometatarsus. If this is considered with the distinct, excavated muscle attachments discussed above, it is suggestive of a powerful pelvic limb, more so than in most vulturids, reminiscent of some accipitrids. Certainly the interpretation of this is very tentative (see Fisher, 1945; Becker, 1985b), but possibly Pliogyps sp. from the Love Bone Bed was more rapacious than other living or fossil vultures, as rapacious birds tend to have a higher flexor ratio than do non-rapacious birds of equal size. As additional fossil material of this species becomes available, this suggestion should be examined further.

Campbell and Tonni (1983) develop further ideas of Prange et al. (1979) on the correlation between the cross-sectional area of the tibiotarsus of a given species and its live weight. They empirically determined the following regression

$$\log Y = 2.54 \log X - 0.19906$$

where Y is the live body weight (gms) and X is the least shaft circumference of the tibiotarsus (mm). The correlation coefficient for this relationship is 0.986, showing that the predictions of the live weight should be very accurate. The least shaft circumference of Pliogyps species (UF 25886) from the Love Bone Bed is 32 mm yielding a predicted weight of 5.2 kg. Sarcoramphus papa, which has a tarsometatarsus approximately as long as this species, weights between 3.0 and 3.75 kg (5 individuals, Brown and Amadon, 1968). This supports

Tordoff's (1959:341ff) conclusions that Pliogyps is relatively a very heavy-bodied, short-legged bird.

The intergeneric relationships of living and fossil vultures in general, and Pliogyps in particular, are very difficult to determine, owing to a paucity of pre-Pleistocene fossil specimens required to determine believable character states. Pliogyps shares tarsometatarsal characters with Sarcoramphus (anterior fossa continuing down shaft to the distal foramen, a similar size of the distal foramen and a similar shape of the hypotarsal ridge). Characters in which Pliogyps differs from Sarcoramphus include the degree of elevation of trochlea III (proximal border merging smoothly with shaft (plantar surface) in all modern skeleton of Sarcoramphus examined), and the amount of excavation of the lateral parahypotarsal sulcus. Pliogyps also shares characters with Vultur and Gymnogyps including the lateral side of the area proximal to trochlea IV being inclined, and the excavation of the anterior fossa extending to the distal foramen (although to a lesser degree than in Sarcoramphus).

Remarks on the Family Vulturidae.

Ligon (1967) and Rea (1983) discuss the relationships of the family Vulturidae with other avian families. There have been many fossil species described as vultures; these are listed in Brodkorb (1964b). Those which have been subsequently moved to other families and orders include: Lithornis vulturinus Owen, volant paleognath (Olson, ms.); Palaeogyps prodromus Wetmore and Neocathartes grallator Wetmore, Family Bathornithidae (Olson, ms.). Olson (ms.) also considers several other "vultures", not to be sufficiently diagnostic to be maintained in this

family. They include: Eocathartes robustus Lambrecht, (too crushed); Teracus littoralis Aymard, (incertae sedis; Olson 1978); and Phasmagyps patritus Wetmore.

This leaves Diatropornis ellioti (Milne-Edwards) and Pleiocathartes europaeus Gaillard from the late Eocene and early Oligocene of the phosphorites du Quercy as the oldest certain records of vultures in Europe. Also known is Plesiocathartes? gaillardi from the early Miocene of Spain and an unreported specimen of a large member of this family from the early Oligocene of Mongolia (Kurochkin, in litt., to Olson, ms.).

In South America, the oldest current record of this family is Dryornis pampeanus Moreno and Mercerat, from the Monte Hermoso Formation in Argentina. This species was originally described as a species of phorusrachid, but was later moved to the family Vulturidae (Brodkorb, 1967). Tonni (1980) states that it is close to the living Vultur. I also note that Campbell (1979) synonymized the fossil Vultur patruus Lönberg, from the Pliocene of Tarija, Bolivia, with the living Vultur gryphus.

In North America, the oldest records of vultures are Sarcoramphus kernensis from the late Miocene (mid-Hemphillian) of Kern River, California, the species of Pliogyps from the Love Bone Bed local fauna, discussed above, and an unreported species of vulturid from the mid-Barstovian Sharkstooth Hill local fauna (Howard, in litt., 1984).

Sarcoramphus kernensis was originally described, and is still only known, from a crushed distal end of a humerus. It was compared only with S. papa (then Vultur papa). It should be re-examined and differentially diagnosed to determine its correct generic position. There are several described species of vultures from the Pliocene and Pleistocene of North

America which are listed in Brodkorb (1964b). Exactly how many of these species are valid remains to be determined.

The earliest certain records for this family are therefore of late Eocene and early Oligocene age in Europe and Asia; of mid to late Miocene age in North America; and of Pliocene age in South America. The fossil record would therefore suggest that this family had an Eurasian origin, then invaded North America, and more recently South America.

An examination of the characters and proportions of the tarsometatarsus and their variation in living and Neogene fossil species suggests that the genera of vultures are oversplit. I agree with Mayr and Short (1970) that Vultur Linnaeus and Gymnogyps Lesson (including G. ampulus, G. howardae, and G. californianus) are congeneric. As Figure 4.4 and 4.5 show, the proportions of the tarsometatarsus of these species differ little from each other. I would also tentatively include Breagyps L. Miller and Howard and Geranogyps Campbell in the genus Vultur Linnaeus, as they too are large vultures with similar tarsometatarsal proportions.

However, I strongly disagree with Mayr and Short's (1970) opinion that Pliogyps Tordoff should be included within the genus Vultur. The tarsometatarsi of both species of Pliogyps differ greatly from Vultur in proportions (Figure 4.4 and 4.5).

Therefore, on tarsometatarsal proportions, I would recognize the following genera: Cathartes Illiger, Coragyps Geoffroy, Sarcoramphus Duméril, Pliogyps Tordoff, and Vultur Linnaeus, (including Gymnogyps, Breagyps, and Geranogyps). If other skeletal elements show a similar trend, I would urge adoption of these genera and their use as described above.

Antilliovultur Arredondo was described from a late Pleistocene cave deposit in Cuba. The type is a 42.5 mm tarsometatarsal fragment which lacks both the proximal end and the distal one-half of the bone. It is also known from a referred distal portion of a humerus, a trochlea IV of a tarsometatarsus, and a single cervical vertebra. The description (Arredondo, 1976) does not clearly differentiate this material from that of the genus Vultur.

Figure 4.b. Plot of greatest length (LENGTH) versus width of proximal end (W-PROX) of the tarsometatarsi of the following species of vultures: (1) Vultur gryphus, (2) Sarcogyps pagei, (3) Gymnogyps californianus, (4) Coragyps atratus, (5) Cathartes aura, (A) Pliogyps fisheri, (B) Pliogyps sp. from the Love Bone Bed L. f., (C) Bredigyps clarki, (D) Teranogyps reliquus, (E) Gymnogyps howardae, and (F) Gymnogyps amplius.

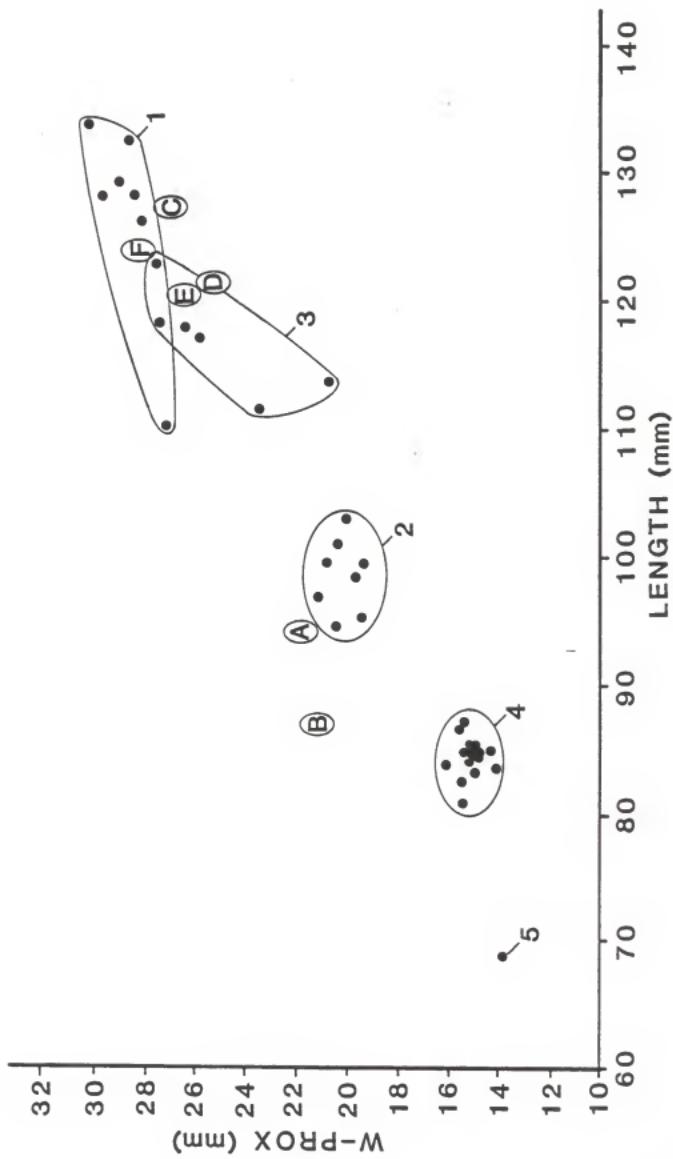


Figure 4.5. Ratio diagram (after Simpson et al. 1960) of measurements of the tarsometatarsi of the following species of vultures: (A) Cathartes aura, (B) Coragyps atratus atratus, (C) Pliogyps sp. from the Love Bone Bed 1. f., (D) Pliogyps fisheri, (E) Sarcocarphus papa, (F) Gymnogyps californianus, (G) Geranogyps melanurus, (H) Gymnogyps howardae, (I) Vultur gryphus, and (J) Breeding Clarki. Measurements, defined in the methods section, are abbreviated as follows: (1) LENGTH, (2) W-PROX, (3) D-PROX-L, (4) FLEXOR, (5) W-SHAFT, (6) D-SHAFT, (7) W-TRILL, (8) D-TRILL, (9) W-DIST.

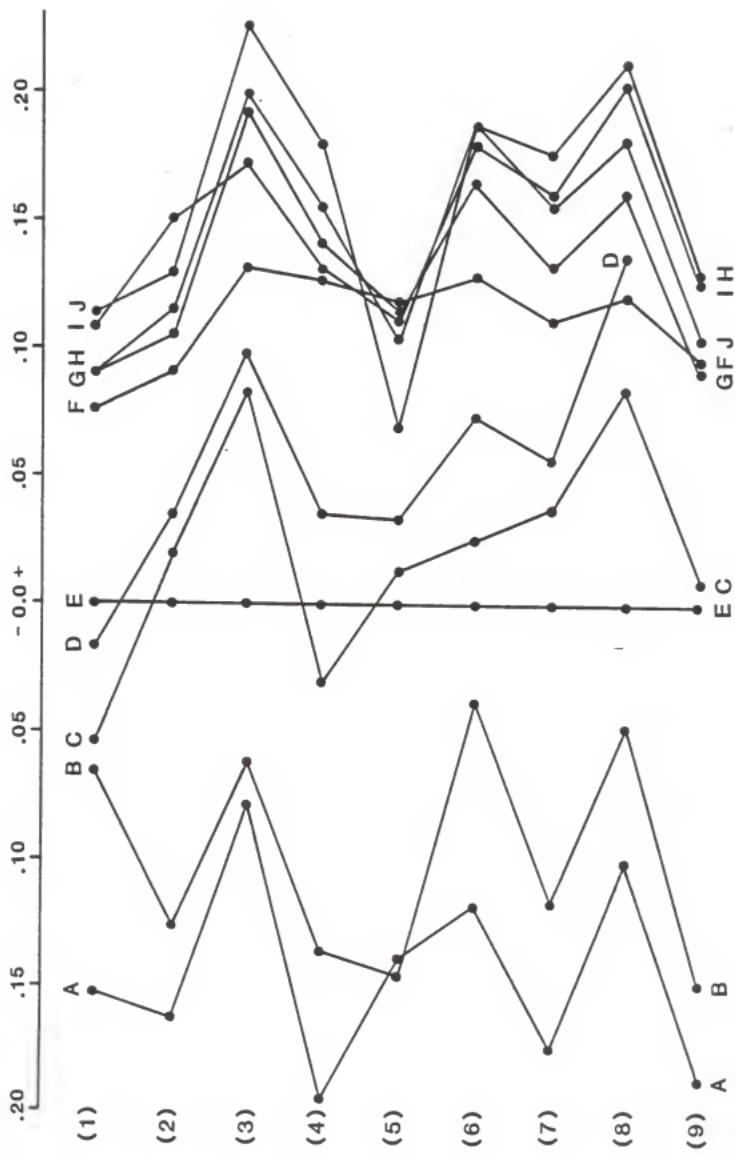
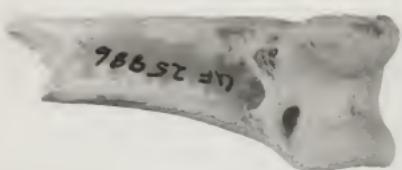


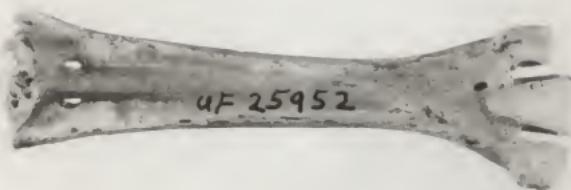
Figure 4.6. Pliogyps sp. A, B. UF 25886, distal end left tibiotarsus. A. Caudal view. B. Cranial view. C, D. UF 25952, right tarsometatarsus. C. Plantar view. D. Dorsal view. Scale A, B = 3 cm.; C, D = 5 cm.



A



B



C



D



Table 4.17. Measurements of the tibiotarsi and tarsometatarsi of the vultures *Coragyps atratus atratus* ($N = 16$, 8 males, 8 females), *Pliogyps fisheri* (holotype) from the Rexroad local fauna, and *Pliogyps* undescribed species from the Love Bone Bed. Data are mean \pm standard deviation and range. Abbreviations are described in the methods section.

Measurements	<u><i>Coragyps a. atratus</i></u>	<u><i>Pliogyps fisheri</i></u>	<u><i>Pliogyps sp.</i></u>
Tibiotarsus			
W-DIST-CR	12.79 ± 0.41 $12.1 - 13.6$	--	--
D-MCON	13.67 ± 0.41 $13.2 - 14.6$	--	--
Tarsometatarsus			
LENGTH	84.43 ± 1.54 $80.4 - 87.1$	94.0	86.6
W-PROX	15.11 ± 0.53 $14.1 - 16.2$	21.9	21.1
D-PROX	11.71 ± 0.42 $11.1 - 12.4$	--	--
W-DIST	16.59 ± 0.57 $15.6 - 17.6$	33.0	--
W-TRIII	6.43 ± 0.21 $6.0 - 6.7$	9.6	9.2
D-TRIII	9.99 ± 0.32 $9.4 - 10.6$	15.2	13.5

Table 4.18. Ratios of intertarsal flexion and tarsometatarsal robustness of species of vultures. Flexion ratio is calculated by (FLEXOR + LENGTH) X 100; Robustness ratio calculated by (W-SHAFT + LENGTH) X 100. Increasing values are correlated with increasing force of flexion and increasing robustness, respectively. (*) approximate.

<u>Species</u>	<u>LENGTH</u>	<u>FLEXOR</u>	<u>W-SHAFT</u>	<u>FLEXION</u>	<u>ROBUSTNESS</u>	<u>RATIO</u>
<u>P. undesc. sp</u>	86.6	14.9	10.8	17.2	12.4	
<u>P. fisheri</u>	94	14.5	11.4	15.4	12.1	
<u>S. papa</u>	*97	*16	*10.5	*16.5	*10.8	
<u>G. californica</u>	*116	*22	*13.5	*19.0	*11.6	
<u>V. gryphus</u>	*126	*22	*14	*17.4	*11.1	
<u>C. atratus</u>	88.4	12.8	7.2	14.5	8.1	
<u>C. aura</u>	65.9	11.3	7.5	17.1	11.4	

Family Pandionidae (Sclater and Salvin, 1893)

Remarks. The following account briefly establishes the presence and distribution of the late Miocene and early Pliocene ospreys in Florida for the paleoecological and biochronological aspects of this study. Detailed descriptions and systematic remarks may be found in Becker (1985b).

Genus Pandion Savigny, 1809

Pandion lovensis Becker, 1985

Material. Love Bone Bed local fauna; UF 25950, nearly complete left tarsometatarsus (holotype); UF 25766, distal half right femur; UF 25884, distal end of right tibiotarsus; UF 25928, complete left tibiotarsus; UF 25863, right tarsometatarsus lacking proximal end; UF 26055, UF 26056, UF 29660, ungual phalanges (paratypes).

Remarks. This species is more generalized, with longer and more slender pelvic limb elements, than the living Pandion haliaetus. See additional comments in Becker (1985b).

Pandion sp.

Material. Bone Valley Mining District, Palmetto Mine; UF 12346, ungual phalanx (claw).

Remarks. This specimen is not identifiable to species, but is sufficiently distinct to document a species of Pandion being present in the Bone Valley Avifauna.

Remarks on the Family Pandionidae.

Warter (1976) has reviewed the fossil history of this family and described the first fossil species of Pandion from the mid-Barstovian Sharkstooth Hill local fauna, California. Recently, another fossil

species of Pandion was described from the late Clarendonian Love Bone Bed local fauna and a phylogeny was proposed for this family (Becker, 1985b).

Family Accipitridae (Vieillot, 1816)

Genus Haliaeetus Savigny, 1809

? Haliaeetus sp.

Material. Bone Valley Mining District, Palmetto Mine; UF 21136, distal end left humerus. Fort Green Mine; UF 55819, distal end left tibiotarsus; UF 61956, distal end left tibiotarsus.

Description. Humerus similar in size and morphology to a small Haliaeetus l. leucocephalus. Provisionally assigned to the genus Haliaeetus. Distinguished from Necrosyrtes and Neophron by having a broader attachment for the anterior articular ligament. Distinguished from Aquila, Necrosyrtes, and Neophron by having a narrow intercondylar furrow (=incisura intercondylaris).

Tibiotarsi also the size of the modern Haliaeetus l. leucocephalus. There is little variation in size between the two tibiotarsi. UF 55819 has a slightly more slender shaft and a more horizontally placed tendinal bridge.

Remarks. The distal tibiotarsus is rather undiagnostic in accipitrids (Jollie, 1976-1977: 226-227), although it has been used in the past to define species. This material is tentively assigned to Haliaeetus on size, overall similarity, and the differences noted above. The variability of the characters used above has not been determined. Additional analysis of the characters used by Rich (1980) to separate the various subfamilies and genera of accipitrids is needed before this material can be correctly placed within this family.

Genus Buteo Lacépède, 1799Buteo near B. jamaciensis (Gmelin, 1788)

Material. Withlacoochee River 4A local fauna; UF 67808, complete left femur.

Description. Size of Buteo jamaciensis harlani. Compares well with this subspecies in overall size, position of intermuscular lines. Differs by having a more narrow patellar sulcus, a slightly more constricted femoral head, greatest length slightly less, and slightly more gracile.

Remarks. This specimen has been reported in Becker (1985a).

Genus Aquila Brisson, 1760Aquila sp. A

Material. Bone Valley Mining District, Hookers Prairie Mine, UF 57299, distal end left tarsometatarsus with posterior wing of trochlea IV broken off.

Description. Virtually indistinguishable from the range of variation of that of the living Aquila chrysaetus in size and morphology. Differs by having a more laterally compressed distal foramen and a slightly deeper tendinal groove (= outer extensor groove of Howard, 1980).

Accipitrid, Genus indet., species A.

Material. Love Bone Bed local fauna, UF 29676, proximal end right carpometacarpus.

Description. Similar in size to a large Haliaeetus leucocephalus or a small Aquila chrysaetus. Carpometacarpus agrees with A. chrysaetus by having a large process on metacarpal I (small in Haliaeetus) and shape of

the distal portion of the carpal trochlea. *Carpometacarpus* agrees with *Haliaeetus* by having a small anterior carpal facet; tendinal groove more on the external surface and having a similar excavation on external side of pollical facet.

Remarks. Material now available is not diagnostic to the generic level. As additional material becomes available, this carpometacarpus should be re-examined to determine its generic status. The time interval between the Love Bone Bed and the Bone Valley local faunas make it unlikely, although not impossible, that these specimens represent one of the species of eagle from Bone Valley.

Accipitrid, Genus indet., species B.

Material. Bone Valley Mining District, Chicora Mine; PB 8100, distal end right carpometacarpus.

Remarks. Carpometacarpus badly fractured and warped. It resembles *Haliaeetus* but this material is not complete enough to discriminate between *Haliaeetus* and species of *Aquila* of similar size.

Accipitrid, Genus indet., species C.

Material. Love Bone Bed local fauna; UF 25491, distal end left tarsometatarsus, lacking half of trochlea III and all of trochlea IV.

Remarks. Typical accipitrid tarsometatarsus. Size between males and females of *Buteo jamaciensis borealis*; but also within the size range of the Neotropical *Spizaetus ornatus* and of several African species of the genera *Lophaetus*; *Hieratus* and Old World species of *Aquila*, including *A. rapax* and *wahlbergi*. The incompleteness of the specimen and the lack of diagnostic characters on the distal end of the tarsometatarsus (Jollie, 1976-1977:266) prevents assignment of this specimen to a genus.

Owing to the long time interval between the Bone Valley local faunas and the Love Bone Bed, it is unlikely that this specimen represents one of the Bone Valley eagles.

Accipitrid, Genus indet.

Material. Withlacoochee River 4A local fauna; UF 67809, pedal phalanx I, digit I; Bone Valley Mining District, District Grade (Agrico) Mine; UF 57303, ungual phalanx (claw); Fort Green Mine, UF 61957, pedal phalanx I, digit I (?); Palmetto Mine, UF 21123, UF 21125, ungual phalanges (claws).

Remarks. All material is representative of a large accipitrid, but is undiagnostic at the generic level.

Remarks on the Family Accipitridae.

The family Accipitridae had approximately 205 Recent species and 62 fossil species when Brodkorb published his Catalogue of Fossil Birds (1964). Other species have been described since then. The systematics of this family is based primarily on external characters (Brown and Amadon, 1968), and probably does not accurately reflect the evolution of this diverse group. Several recent studies (Jollie, 1976-1977; Rich, 1980) have described, in exhaustive detail, the morphology of this family. But at the present, there is not a phylogeny of the family as a whole based on internal morphology (but see comments in Olson, in press; and Jollie, 1976-1977:309ff).

In Florida, there is also unreported accipitrid material from the Hemingfordian Thomas Farm l. f. and from several late Pleistocene localities (Campbell, 1980; Carr, 1981).

Order Anseriformes (Wagler, 1831)Family Anatidae Vigors, 1825

Remarks. There is a large amount of fossil material representing anatids from nearly all local faunas included in this study, especially from the Love Bone Bed local fauna. Unfortunately, much of it consists of fragmentary, waterworn specimens or specimens of slight diagnostic value (radii, ulnae, vertebrae, etc.). The correct taxonomic assignment of these specimens is further complicated by the presence of both goose-like ducks (Anatinae: Tadornini) and duck-like geese (Anserinae: Dendrocygnini) which precludes assigning specimens to subfamily on the basis of size. Therefore, I do not assign material to a taxonomic rank and list it under referred material unless it is clearly diagnostic. The classification proposed by Woolfenden (1961) is followed.

Subfamily Anserinae Vigors, 1825

Tribe Dendrocygnini Reichenbach, "1850"

Genus Dendrocygna Swainson, 1831

Generic characters. The coracoids of Dendrocygna may be distinguished from those of all other anseriform genera by the presence of a pit-like depression on the ventro-lateral surface of the sternal end. Other characters of the coracoid are listed in Woolfenden (1961). The carpometacarpus of Dendrocygna may also be distinguished from all other anseriform genera by its narrow and elongate proportions, the metacarpal II incurved in dorsal view, the external rim of the carpal trochlea only slightly notched, and a prominent neck present between the carpal trochlea and metacarpal III (Woolfenden, 1961).

Dendrocygna sp.

Material. Love Bone Bed local fauna; UF 25992, UF 25997, UF 29765, UF 29766, right coracoids; UF 29764, UF 29763, UF 25803, left coracoids; UF 29762, UF 25774, UF 25839, humeral ends left coracoids (tentatively referred); UF 25845, humeral end right coracoids (tentatively referred); UF 25755, left carpometacarpus, missing metacarpal III, UF 25757, prominent end left carpometacarpus.

Remarks. Coracoids and carpometacarpus (Fig. 4.7) typical of Dendrocygna as described by Woolfenden (1961). I have been unable to find either qualitative or quantitative characters which will distinguish the fossil specimens from the Love Bone Bed from the few specimens of the Recent species of Dendrocygna available, when the variation of modern populations is taken into account. Measurements are given in Table 4.19.

Fossil species in this tribe include Dendrochen robusta A. H. Miller, based on humeri from the early Hemingfordian Flint Hill local fauna, South Dakota; and Dendrocygna evera Wetmore, based on a proximal humerus from the Blancan Benson local fauna, Arizona. Dendrocygna validipinnis DeVis, from the Pleistocene of Australia was shown by Olson (1977a) to be a junior synonym of Biziura.

Recently, Cheneval (1984) transferred three species previously referred to Anas from St.-Gérand-le-Puy to the genus Dendrochen as D. blanchardi, D. consobrina and D. natator. He also noted a possible relationship between Romainvillia and Dendrochen.

Dendrocygna is predominately tropical, with the greatest diversity of species occurring in the New World tropics and southeastern Asia. Two species (D. vidiuata and D. autumnalis) occur in both the Old World and

New World tropics. D. autumnalis is widely distributed, highly discontinuous, with no constant geographical variation (Friedmann, 1947).

Tribe Anserini Vigors, 1825

Genus Branta Scopoli, 1769

?Branta sp. A.

Material. Love Bone Bed local fauna; UF 29751, proximal end right humerus; UF 29752, distal end right humerus; UF 25797, left coracoid; UF 26005, humeral end right coracoid; UF 25748, UF 25751, proximal ends right carpometacarpi; UF 25890, UF 25891, distal ends left tibiotarsi; UF 25951, UF 29759, nearly complete left tarsometatarsi.

Remarks. Skeletal elements about the size of those of the Recent Branta canadensis interior. Assignment to Branta is based on the following characters: proximal humerus with the attachment of the M. triceps externus with a distinct border; coracoid with furcular facet not deeply undercut, with only a few pneumatic foramina present (Woolfenden 1961:49). This assignment is tentative, as similar character states are approached in specimens of Anser species. Other elements were arbitrarily assigned on the basis of size.

Anserinae, Genus indet. sp. B.

Material. Love Bone Bed local fauna, UF 29753, left carpometacarpus without metacarpal III; UF 25754, proximal end right carpometacarpus; UF 25758, proximal end left carpometacarpus; UF 29761, right coracoid; UF 25904, distal end right tibiotarsus; UF 25879, distal end left tibiotarsus; UF 25929, UF 25947, distal ends left tarsometatarsi.

Remarks. Skeletal elements about the size of those of the living males of Anser albifrons. Material badly waterworn, leaving no diagnostic characters to permit assignment to genus.

Anserinae, Genus indet. sp. C. (or B.?)

Material. Love Bone Bed local fauna; UF 25750, proximal end right carpometacarpus; UF 25763, distal end right carpometacarpus.

Bone Valley Mining District, near Brewster; PB 174, proximal end left carpometacarpus.

Remarks. The above skeletal elements are approximately the size of those of Anser rossii. These elements may represent Anserinae, genus and species indet. sp B. (above), depending upon how much size variation is allowed within a single fossil species.

Anserinae, Genus indet. sp. D

Material. Bone Valley Mining District, specific locality unknown; UF 61598, left coracoid.

Remarks. Coracoid much smaller than that of Anser rossii (or species B or C above). Furcular facet deeply undercut as is typical of the tribe Anserini (Woolfenden, 1961).

Subfamily Anatinae (Vigors, 1825)

Remarks. A large amount of material of anatines exists from nearly all the localities included in this dissertation, but it is not of sufficient diagnostic character to allow further identification. Rather than arbitrarily assign specimens to size categories which would not reflect the true species composition, I prefer to leave this material undesignated pending further investigations of the anatid material from

other Neogene fossil localities in North America which have not been included within this study.

Tribe Tadornini Reichenbach, "1850"

Remarks. The humerus of the tribe Tadornini may be distinguished by the following combination of characters: capital shaft ridge prominent, directed forward toward the external tuberosity. Characters that are typical anatine in form are also present, such as having the external head of the M. humerotriceps deeply undercutting the humeral head and being continuous with the capital groove.

Genus and species indet.

Material. Bone Valley Mining District, Ft. Green Mine (# 13 dragline); UF 57253, proximal end right humerus.

Remarks. Typical Tadornine humerus about the size of that of a male Chloephaga picta. This specimen could represent a large species in the genus Anabernicula, but it is apparently larger than all species now described in that genus. The specimen is not complete enough to warrant assignment to genus.

Tribe Anatini Vigors, 1825

Genus Anas Linnaeus, 1758

Anas undescribed sp. A.

Material. Love Bone Bed local fauna; UF 25738, complete left humerus, UF 25720, left humerus missing distal end, UF 29750, proximal end left humerus; UF 25731, 25736, proximal ends right humeri; UF 25837, UF 25853, UF 29770, UF 29761, complete right coracoids; UF 25805, UF 29768, complete left coracoids; UF 29801, UF 25840, UF 25841, humeral ends right coracoids (tentatively referred); UF 25795, UF 25780, UF 29795,

humeral ends left coracoids (tentatively referred); UF 25756, left carpometacarpus missing shaft of metacarpal III.

McGehee Farm local fauna; UF 8780, complete left coracoid; UF 12469, right tarsometatarsus.

Description. The above taxonomic assignment is based primarily on humeri. They are referable to the Anatinae by lacking a prominent capital shaft ridge, having the capital groove extending laterally across the anconal surface and deeply undercutting the humeral head, and by having a strongly developed attachment for the external head of the triceps.

Within the subfamily Anatinae, the fossil humeri may be distinguished from those of the tribe Tadornini by lacking a prominent capital ridge shaft, by having the head unrotated, deltoid crest not large and flaring and not extending distally. They may also be distinguished from those of the tribe Cairinini by not having a robust shaft and the pneumatic fossa not restricted to a circular opening rimmed with heavy bone; distinguished from those of the tribe Oxyurini by having a very deep pneumatic fossa, extending well under head without numerous foramina piercing the walls, by the entepicondyle not being reduced, and by the scar for the attachment of the latissimus dorsi posterioris not being in a line with the outer edge of the pectoral attachment; distinguished from those of the tribe Mergini and the tribe Somaterini by the internal tuberosity not being short and deep, and by the entepicondylar prominence not being reduced.

The fossil humeri from the Love Bone Bed local fauna agree with the humeri of both the Anatini and the Aythini by having the capital ridge shaft obsolete and by having the pneumatic fossa ovaloid and unrimmed

with heavy bone. The fossil humeri particularly agree with the humeri of the Anatini by having the impression of the brachialis not well defined (Aythini with impression well-defined, with a distal medial rim sharp) and by having the entepicondyle approximately equal in anconal height to the ectepicondyle (Aythini with entepicondyle distinctly higher). In three out of five fossil specimens, the pneumatic fossa is open and contains struts (as in Anatini; in Aythini it is usually closed). Distal end rotated medially as in Anas. Greatest morphological resemblance of the humerus, coracoid, carpometacarpus, and tarsometatarsus is to the genus Anas (Fig. 4.7).

Comparisons were made with the smallest living species of Anas, Anas hottentata, to illustrate the morphological characters of this extremely small fossil species from the late Miocene of Florida (see Table 4.20). The humeri from the Love Bone Bed are smaller, less robust, but with deltoid crest similar. The coracoids from the Love Bone Bed are smaller, proportionally more stout, with the medial margin (in ventral view) slightly inflated. Carpometacarpus from the Love Bone Bed is much smaller, and more gracile. Tarsometatarsus from McGehee Farm is smaller, more slender, with the lateral parahypotarsal sulcus more excavated. Sulcus on anterior surface proximal to canal more defined.

Remarks. The above specimens agree with the genus Anas in all characters except one--whether the humerus has an open or closed pneumatic fossa. The two extremes of this character are one of the defining characters which distinguish the tribes Anatini and Aythini (Woolfenden, 1961: 12). This site is the entrance of the air sac system into the shaft of the humerus and is highly adaptive as it allows for the additional regulation of buoyancy in diving birds. It almost certainly

evolved more than once, as evidenced by its being open in some genera of mergansers (always open in Mergus, almost always open in Lophodytes) and closed in others (Mergellus) (Woolfenden, 1961).

Before the exact systematic position of this species can be determined, additional comparisons are needed with small living and fossil species of Anas. Of special interest is Anas luederitzensis Lambrecht 1929, from the mid-Tertiary of southwest Africa. This species is said to be distinguished from Anas querquedula and Anas cyanoptera by having a pneumatic fossa not markedly perforated as in most anatids (Howard, 1964).

?Anas, size near A. acuta

Material. Love Bone Bed local fauna; UF 26001, right coracoid; UF 25798, UF 25799, UF 25800, UF 25801, left coracoids.

McGehee Farm local fauna; UF 9481, UF 31784; right coracoids; UF 9486, UF 9489, left coracoids.

Remarks. Typical Anas morphology. Skeletal elements slightly larger than A. acuta; definitely smaller than modern specimens of Anas platyrhynchos.

Anatinini, Genus indet., species A.

Material. Love Bone Bed local fauna; UF 29767, complete left coracoid; UF 25808, UF 25854, humeral ends coracoids, tentatively referred.

Remarks. Coracoids proportionally long and slender; slightly smaller than females of A. crecca carolinensis. See remarks below under "Genus indet., sp. B."

Anatini, Genus indet., species B.

Material. Love Bone Bed local fauna; UF 25791, left coracoid; UF 25791, UF 25786, UF 25852, humeral ends coracoids, tentatively referred.

Remarks. Similar morphology as described above for genus and species indet sp. A, but slightly larger than the coracoids of the males of A. crecca carolinensis. This material probably represents the same species as "A" above, but of the opposite sex.

Tribe Aythini (Delacour and Mayr, 1945)

Genus Aythya Boie, 1822

Aythya sp. A

Material. Bone Valley Mining District, Ft. Green Mine (#13 dragline); UF 49695, right carpometacarpus; UF 53945, proximal end right carpometacarpus; Palmetto Mine; UF 21124, left coracoid, (tentative referred); Ft. Green Mine (#6 dragline); UF 53866, left coracoid, (tentatively referred); specific locality unknown, UF 61599, Left coracoid, (tentatively referred).

Remarks. Size similar to that of Aythya collaris. Carpometacarpus referred to this tribe by lacking the distal swelling on the external rim of the carpal trochlea (Woolfenden, 1961). Coracoids tentatively referred here because of general overall similarity with Aythya in characters (Woolfenden, 1961).

Tribe Mergini (Swainson, 1831)

Genus Bucephala Baird, 1858

Bucephala ossivallis Brodkorb, 1955

Material. Bone Valley Mining District, Palmetto Mine (= locality 2 of Brodkorb, 1955a); PB 172, humeral end left coracoid (holotype).

Remarks. Brodkorb (1955a) states that this coracoid agrees with that of Bucephala clangula in general appearance and details of the brachial tuberosity, but differs by being smaller and in details of the procoracoid and triosseal canal.

Anatids are fairly rare members of the Bone Valley avifauna. As additional material becomes available, this poorly known species should be re-examined.

Tribe Oxyurini J. C. Phillips, 1926

Genus Oxyura Bonaparte, 1828

Oxyura cf. O. dominicus

Material. Bone Valley Mining District, Ft. Green Mine; UF 61950, proximal ends left humerus.

Remarks. Size of a small Oxyura dominicus. Humeral head slightly more undercut by the external head of the m. triceps in the fossil specimen than in the series of recent skeletons of O. dominicus. All other characters within the range of variation of O. dominicus.

Remarks on the Family Anatidae.

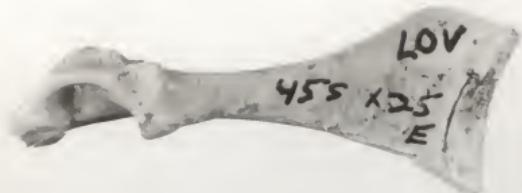
Howard (1964, 1973) has reviewed the extensive fossil record of the Anatidae, so there is little need once again to review all taxa covered by Howard. New Miocene fossil species described since 1973 include Cygnopterus alphonsi from the Aquitanian of St.-Grand-le-Puy, France by Cheneval (1984); and a Blanican goose from the Broadwater local fauna, Anser thompsoni by Martin and Mengel (1980). Both of these species are known from several elements.

Four new species have also been described from the late Pleistocene. Anas schneideri was described from a single carpometacarpus from the

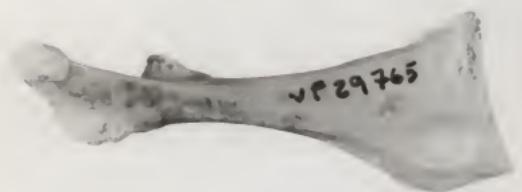
Rancholabrean Little Box Elder local fauna (Emslie, 1985). This species is significantly smaller than the living A. crecca. Anas schneideri is near the size of A. pullulans described from the mid to late Clarendonian Black Butte local fauna, Oregon, but differs from this species by having metacarpal I relatively higher (Emslie, 1985). Campbell (1979) described three new species of Anas (A. talarae, A. amotape, and A. sanctahelenae) from the late Pleistocene of Bolivia and Ecuador. Differences between these South American species of Anas and other living species of Anas seem slight. Campbell (1979) also described, from the same localities, a new genus and species (Nannonetta invisitata) of Tadorine.

Anatids are rare as fossils until the Neogene. Olson (ms) notes that the major adaptive radiation of anatids took place in the Miocene; for it is difficult to place fossils before this time in modern tribes and genera.

Figure 4.7. Dendrocygna sp. A, B. Right coracoid, UF 29765.
A. Dorsal view. B. Ventral view. C, D. Left carpometacarpus, UF
25755. C. Ventral view. D. Dorsal view. Scale = 2.5 cm.



A



B



C



D

Figure 4.8. *Anas* sp. A, B. Left coracoid, UF 25805. A. Dorsal view. B. Ventral view. C, D. Left carpometacarpus, UF 25756. C. Ventral view. D. Dorsal view. E, F. Left humerus, UF 25738. E. Cranial view. F. Caudal view. Scale (top) A-D = 2 cm.; (bottom) E, F = 3 cm.

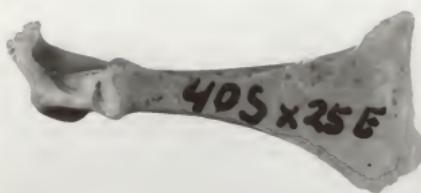
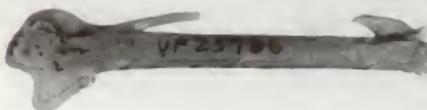
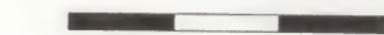
A**E****B****C****D****F**

Table 4.19. Measurements of the coracoids and carpometacarpi of Dendrocygna viduata (N = 8, 4 males, 4 females), Dendrocygna arborea (N = 4, 1 male, 3 females, maximum), Dendrocygna bicolor (N = 9, 6 males, 3 females, maximum), Dendrocygna autumnalis (N = 8, 4 males, 4 females), and Dendrocygna species from the Love Bone Bed local fauna. Data are mean \pm standard deviation (number) and range. Abbreviations are defined in the methods section.

Measurement	<u>D. viduata</u>	<u>D. arborea</u>	<u>D. bicolor</u>	<u>D. autumnalis</u>	<u>Dendrocygna</u> sp.
Coracoid					
HEAD-IDA	40.79 \pm 1.74 38.6 \pm 44.3	44.98 \pm 1.97 42.9 \pm 46.8	42.14 \pm 3.97 37.8 \pm 52.1	42.46 \pm 1.61 40.1 \pm 44.8	44.93 \pm 1.97 (6) 42.1 \pm 47.9
HEAD-CS	14.75 \pm 0.88 14.1 \pm 16.8	15.18 \pm 1.30 13.5 \pm 16.6	15.01 \pm 0.49 14.3 \pm 15.8	15.26 \pm 0.65 14.5 \pm 16.3	15.78 \pm 0.87 (9) 13.8 \pm 16.8
D-HEAD	3.79 \pm 0.16 3.5 \pm 4.0	4.00 \pm 0.28 3.8 \pm 4.0	3.44 \pm 0.17 3.2 \pm 3.7	3.80 \pm 0.30 3.4 \pm 4.3	4.10 \pm 0.39 (8) 3.8 \pm 5.0
W-SHAFT	3.69 \pm 0.07 3.6 \pm 3.8	4.18 \pm 0.17 4.0 \pm 4.4	4.01 \pm 0.42 3.3 \pm 4.5	4.10 \pm 0.21 3.8 \pm 4.5	4.46 \pm 0.32 (10) 4.1 \pm 5.0
D-SHAFT	3.60 \pm 0.29 3.2 \pm 4.0	3.68 \pm 0.17 3.5 \pm 3.9	3.77 \pm 0.17 3.6 \pm 4.4	3.86 \pm 0.19 3.6 \pm 4.0	4.28 \pm 0.38 (10) 3.8 \pm 5.0
FAC-IDA	14.24 \pm 0.64 13.4 \pm 15.1	16.57 \pm 0.50 16.1 \pm 17.1	14.94 \pm 0.82 13.6 \pm 16.3	15.68 \pm 0.64 14.6 \pm 16.6	16.03 \pm 0.51 (4) 15.5 \pm 16.7
IDA-PP	30.05 \pm 1.20 28.9 \pm 32.7	33.53 \pm 1.53 32.2 \pm 35.0	29.54 \pm 1.17 27.0 \pm 30.7	31.26 \pm 1.45 29.4 \pm 33.4	32.86 \pm 1.13 (7) 31.8 \pm 35.2

Table 4.19--continued

<u>Measurement</u>	<u>D. viduata</u>	<u>D. arborea</u>	<u>D. bicolor</u>	<u>D. autumnalis</u>	<u>Dendrocygna sp.</u>
Carpometacarpus LENGTH	52.95 ± 2.06 51.5 - 57.7	59.70 ± 2.77 56.5 - 61.3	51.93 ± 1.51 49.5 - 54.1	54.63 ± 2.64 50.0 - 58.5	55.0
W-CARPAL	4.79 ± 0.20 4.5 - 5.1	5.57 ± 0.06 5.5 - 5.6	4.54 ± 0.23 4.1 - 4.8	4.90 ± 0.19 4.6 - 5.1	5.2; 5.4
D-PROX	10.60 ± 0.26 10.2 - 11.0	11.70 ± 0.20 11.5 - 11.9	10.66 ± 0.29 10.2 - 11.0	11.30 ± 0.51 10.7 - 12.2	11.3; 11.5
D-SHAFT	3.00 ± 0.18 2.8 - 3.3	3.43 ± 0.06 3.4 - 3.5	3.13 ± 0.19 2.9 - 3.5	3.16 ± 0.24 2.9 - 3.5	3.4; 3.6
W-SHAFT	3.35 ± 0.12 3.2 - 3.5	3.97 ± 0.12 3.9 - 4.1	3.38 ± 0.21 3.1 - 3.7	3.70 ± 0.26 3.3 - 4.1	4.0; 4.4
W-DIST	6.08 ± 0.31 5.5 - 6.5	6.60 ± 0.30 6.3 - 6.9	5.76 ± 0.31 5.4 - 6.1	6.29 ± 0.36 6.0 - 6.9	6.2

Table 4.20. Measurements of coracoids, humeri, carpometacarpi, and tarsometatarsi of males of *Anas hottentata* and *Anas* sp. A from the Love Bone Bed and McGehee local faunas. Data are mean \pm standard deviation and range. Abbreviations defined in methods section.

<u>Measurement</u>	<u><i>Anas hottentata</i></u>	<u><i>Anas</i> sp. A</u>
Coracoid		
HEAD-IDA	29.7; 30.6; 29.7	25.85 ± 0.72 (4) $24.8 - 26.4$
HEAD-CS	9.7; 9.5; 9.7	8.93 ± 0.43 (4) $8.3 - 9.2$
W-SHAFT	3.2; 3.1; 3.0	3.06 ± 0.23 (7) $2.8 - 3.4$
D-SHAFT	2.2; 2.5; 2.6	2.56 ± 0.50 (7) $2.1 - 3.6$
IDA-PP	22.8; 24.0; 22.9	20.37 ± 0.34 (6) $19.8 - 20.7$
L-GLEN	5.8; 6.0; 6.1	6.10 ± 0.23 (7) $5.8 - 6.5$
Humerus		
LENGTH	54.6; 56.2; 54.2	50.8
W-SHAFT	4.1; 4.0; 4.3	3.63 ± 0.31 (4) $3.2 - 3.9$
D-SHAFT	3.5; 3.4; 3.7	3.03 ± 0.49 (4) $2.4 - 3.5$
W-PROX	11.5; 11.6; 11.6	12.2; 11.6
D-PROX	6.2; 6.5; 6.3	6.4; 5.3
D-HEAD	4.1; 4.4; 4.4	3.80 ± 0.13 (4) $3.7 - 4.0$
W-DIST	8.2; 8.3; 8.6	7.8
D-DIST	4.8; 4.8; 5.2	4.8
D-ENTEP	3.5; 3.5; 4.0	4.0

Table 4.20--continued

<u>Measurement</u>	<u>Anas hottentata</u>	<u>Anas sp. A</u>
Carpometacarpus LENGTH	32.7; 32.0	27.9
W-CARPAL	3.3; 3.6	2.9
D-PROX	7.8; 7.8	6.7
L-MCI	4.9; 4.8	4.5
D-SHAFT	2.3; 2.3	2.1
W-SHAFT	2.4; 2.6	2.1
D-DIST	2.8; 3.0	2.2
W-DIST	4.3; 4.2	3.5
Tarsometatarsus LENGTH	27.5; 27.9; 28.1	25.5
W-SHAFT	3.0; 3.1; 2.9	2.8
D-SHAFT	2.4; 2.5; 2.7	2.3
W-PROX	5.4; 5.8; 5.8	5.1
		-

Order Galliformes (Temminck, 1820)Family Phasianidae Vigors, 1825

Subfamily Meleagridinae (Gray, 1840)

Genus indet.

Material. Love Bone Bed local fauna; UF 25768, proximal half left femur.

Remarks. Steadman (1980) reviewed and evaluated the previously used taxonomic characters of the meleagridine femur. The femur of Proagriocharis kimbballensis is not known and that of Meleagris progenes is damaged so that the few qualitative characters of value could not be judged for these species. As there is a general increase in size through time in this subfamily (Steadman, 1980:153), I attempted to assign this specimen to a genus by comparing measurements of Recent and fossil species (Table 4.21). These comparisons assume that similar measurements (e.g. diameters of hind limb elements) do not vary between different skeletal elements of a given species. Ratios of measurements in Proagriocharis kimbballensis to those of Meleagris gallopavo range from about 0.57 to 0.71. In Meleagris progenes these ratios range from 0.76 to 0.84. Ratios for UF 25768 range from 0.60 to 0.64 if the specimen is assumed to be male (within the range of Proagriocharis kimbballensis) or from 0.80 to 0.83 if the specimen is assumed to be female (within the range of Meleagris progenes). This specimen is therefore not assigned to genus.

Genus Meleagris Linnaeus, 1758cf. Meleagris sp.

Material. Bone Valley Mining District, Palmetto Mine; UF 21033, distal end tibiotarsus.

Remarks. I have not been able to locate this specimen, but have followed Steadman (1980:141) for this identification. There is additional material of Meleagris in the UF collections from the Bone Valley Mining District, but it is likely that it originated from Pleistocene deposits.

Remarks on the Family Phasianidae (Subfamily Meleagridinae).

See Steadman (1980) for an in-depth discussion of the osteology, paleontology, systematics, and evolution of the subfamily Meleagridinae.

Table 4.21. Comparative measurements of the femora and tarsometatarsus of the turkeys Proagriocharis kimballensis, Meleagris progenes and Meleagris gallopavo silvestris, and Meleagridinae, genus indet. from the Love Bone local fauna. All measurements are means (Steedman, 1980) except those of the material from the Love Bone local fauna. Ratios were calculated by dividing the measurement in the fossil specimens by that of M. g. silvestris.

Measurement	Sex	Love		Bone Bed		<u>P. kimbballensis</u>		<u>M. progenes</u>		<u>M. g. silvestris</u>	
		Datum	Ratio	Datum	Ratio	Datum	Ratio	Datum	Ratio	Datum	Ratio
Femur	M	20.9	0.603	—	—	—	—	—	—	34.65	1.00
	F	20.9	0.795	—	—	—	—	—	—	26.28	1.00
D-HEAD	M	8.2	0.641	—	—	—	—	—	—	12.79	1.00
	F	8.2	0.830	—	—	—	—	—	—	9.81	1.00
Tarsometatarsus	M	—	—	14.0	0.572	18.7	0.764	24.49	1.00	—	—
	F	—	—	12.95	0.665	—	—	19.46	1.00	—	—
W-SHAFT	M	—	—	—	—	7.45	0.798	9.34	1.00	—	—
	F	—	—	5.05	0.690	—	—	7.32	1.00	—	—
D-SHAFT	M	—	—	—	—	5.05	0.836	6.04	1.00	—	—
	F	—	—	3.5	0.709	3.9	0.789	4.94	1.00	—	—

Order Ralliformes (Reichenbach, 1852)Family Gruidae Vigors, 1825

Remarks. The following elements are so waterworn and abraded that I cannot do more than tentatively refer them to the family Gruidae.

Material. Love Bone Bed local fauna; UF 25966, UF 25967, cervical vertebrae; UF 26086, right digit II, phalanx I (wing); UF 26087, distal end left radius; UF 25761, UF 25762, distal ends left carpometacarpi; UF 29723, UF 25894, distal ends left tibiotarsi; UF 25958, UF 25960, distal shafts left tarsometatarsi; UF 25862, UF 25860, fragmentary distal ends right tarsometatarsi; UF 26032, UF 26033, UF 26034, UF 26036, UF 26037, UF 26038, UF 26039, UF 26040, pedal phalanges.

Generic diagnosis. The following diagnosis is based on an examination of the following genera (number of species in parenthesis): Grus (9), Bugeranus (1), Anthropoides (2), and Balearica (2).

No diagnostic characters noted on portion of the coracoid and carpometacarpus preserved. Femur with proximal portion of the cranial intermuscular line located medially, away from the crista trochanteris in Balearica (extending from the crista trochanteris in other genera examined). Only a few characters on the distal end of the tibiotarsus will separate all species of Grus from all other species of Bugeranus, Anthropoides, and Balearica. In Grus, the lateral surface of the lateral condyle is expanded (less so in other genera), the internal ligamental process is expanded (similar in Bugeranus, less so in Anthropoides, and Balearica). Balearica is distinguished by having the distal end antero-posteriorly flattened, with the medial condyle rotated outward, producing a broad, U-shaped anterior intercondylar sulcus. The proximal end of the tarsometatarsus in Balearica with a short hypotarsus (longer in Grus, Anthropoides (but short in A. virgo), and Bugeranus); Anthropoides with a

transverse sulcus relatively narrow and deeply excavated (less so in Grus, Balearica, and Bugeranus). Distal end of the tarsometatarsus in Balearica with trochlea II higher on shaft than in that of other genera.

Subfamily Gruinae (Vigors, 1825)

Genus Grus Pallas, 1766

Grus sp. A.

Material. Love Bone Bed local fauna; UF 25752, proximal end right carpometacarpus; UF 25903, distal end left tibiotarsus; UF 26092, proximal end right tarsometatarsus.

Description. Tibiotarsal and tarsometatarsal characters as in the genus Grus. Carpometacarpal fragment referred on basis of size. Smaller than all species of living cranes except Grus canadensis. Differs from Grus canadensis by having a less pronounced lateral expansion of the lateral condyle, a less pronounced internal ligamental process, a more robust shaft, a larger tendinal canal, and a broad triangular crest extending proximally from the lateral condyle.

Tarsometatarsus slightly larger than that of Grus canadensis; carpometacarpus slightly smaller.

Remarks. The unexpected difference in size between the above specimens could possibly be due to the elements representing two sexes, two subspecies (analogous to the modern situation in Florida resident population of Grus canadensis pratensis and the migratory Grus canadensis tabida), or a single species of slightly different proportions. With only the scanty material above, it is impossible to choose between these possibilities.

The skeletal elements of the fossil species Grus nannodes from the Hemphillian Edson local fauna, Kansas, is similar in size to the above

specimens. However, in the original description it was not demonstrated that Grus nannodes actually belongs in the genus Grus. With the prevalence of balearicinae-like cranes in the Tertiary of North America, gruid fossil cannot be uncritically assigned to the genus Grus. Therefore "Grus nannodes" should be re-examined before its current taxonomic assignment is accepted.

Grus sp. B

Material. Love Bone Bed local fauna; UF 26002, sternal end right coracoid; UF 29721, humeral end right coracoid; UF 25740, right scapula; UF 25722, UF 25737, distal ends left humeri; UF 25749, right carpometacarpus missing part of shaft of metacarpal III; UF 25753, proximal end right carpometacarpus; UF 29720, proximal end right femur; UF 25887 (tent. referred), UF 25893 (tent. referred), UF 25908, UF 25911, distal ends left tibiotarsi; UF 25885, UF 25896 (tent. referred), UF 29722, distal ends right tibiotarsi; UF 25988, UF 25989, UF 29725, proximal ends left tarsometatarsi; UF 26093, UF 29724, proximal ends right tarsometatarsi; UF 25857, distal end right tarsometatarsi; UF 25931, UF 25944, UF 25945, UF 29726, distal end left tarsometatarsi.

Remarks. Size similar to that of a large Grus americana or Grus japonensis. Coracoids, carpometacarpi, humeri, and femur referred here on the basis of size, as are the several of the above waterworn tibiotarsi.

Distal tibiotarsus with characters of the genus Grus, but also similar to Grus (= Bugeranus) leucogeranus. Larger than Grus canadensis, G. grus, and G. monacha, slightly larger than G. vipio and Grus rubicunda (G. nigricollis not available). Similar in size to G. americana, G.

japonensis, and G. antigone. These last three species have very similar distal tibiotarsi and I have not been able to find consistent qualitative characters on this element to separate these species from each other and from the fossil specimens above. The proximal and distal ends of the tarsometatarsus are also indistinguishable from those of G. americana, G. japonensis, and G. antigone. Two specimens (distal tibiotarsus; UF 25908, UF 25911) are larger than all other fossil specimens and may represent either sexual variation or a specific difference. The lack of an adequate series of skeletons of Recent species prevents determination of this question.

A large species of Grus is known from the Lee Creek local fauna (Olson, ms). Grus sp. B. probably is closely related, or identical with this species.

Subfamily Balearicinae (W. L. Sclater, 1924)

Balearicinae, Genus et. species indet.

Material. Bone Valley Mining District, Nichols Mine; UF 24586, distal end of right tibiotarsus.

Description. Tibiotarsus slightly smaller than that of a female Anthropoides virgo, but having characters typical of the subfamily Balearicinae. Comparisons with the tibiotarsus of an undescribed balearicinae crane from the Hemphillian Long Island local fauna, Kansas, (YPM 4662) shows UF 24586 to share a similar shape and position of the condyles, although UF 24586 is much larger and is more anterior-posteriorly compressed.

Remarks. Comparisons of this tibiotarsus with unpublished fossil material in the Frick and USNM collections shows that this specimen is distinct from that of both Probalearica and Aramornis. Additional

material of balearicine cranes is now under study by Feduccia. As much of this material consists of complete, articulated skeletons, it seems unnecessary to further describe this single, partial element. From the material which I have seen, there are at least two species of balearicinae cranes in North America at the end of the Hemphillian. Based on the above specimen, the last occurrence now known of this subfamily of cranes in North America is from the late Hemphillian Bone Valley local fauna.

Genus Aramornis Wetmore, 1926

cf. Aramornis, sp. A.

Material. Love Bone Bed local fauna; UF 25949, distal end left tarsometatarsus, missing trochlea IV.

Description/ Remarks. Tarsometatarsus compares well with the type of Aramornis longurio (F:AM 6269) in relative proportions and positions of the trochae II and III, but differs by having a larger distal foramen and a greater overall size. See Table 4.25 for measurements. Additional material is needed to verify this generic assignment.

Remarks on the Family Gruidae.

Johnsgard (1983) considers the following species to be closely related: Grus japonensis and G. americana, Grus rubicundus and G. antigone; Bugeranus carunculatus and B. leucogeranus; Antropoides virgo and A. paradisea; and Balearica pavonina and B. regulorum. Additionally, he considers Grus grus, G. monacha, G. canadensis, and G. vipio to form a loose species cluster. Outside of these obvious groupings, he makes no attempt to place them within a phylogeny. With the exception of Wood's (1979) phenetic study, little work has been done concerning the

relationships of the cranes above the species level. Wood's paper (1979) unfortunately adds little new information; rather it addresses the concordance between previously proposed classifications and the clusters produced from multivariate analysis of different suites of characters.

The family Aramidae is here considered to be closely related to the subfamily Balearicinae (Olson, ms). Fossil species of cranes (Gruidae + Aramidae) are numerous throughout much of the Tertiary of North America and Europe. They are listed in Brodkorb (1967), reviewed formally in Cracraft (1973), and reviewed less formally by Olson (ms). Systematic changes to Brodkorb (1967) may be found in the latter two publications.

My survey of mainly unpublished collections in the Frick Collections, American Museum of Natural History, indicates there was a great radiation of balearicinae cranes in North America during most of the Tertiary (Becker, in prep; Olson, in press). Many fossil species originally assigned to the Gruinae should be re-assigned to the Balearicinae; and probably would have been long before now, were this subfamily still extant in North America. The latest known occurrence of this subfamily in North America is from the latest Hemphillian Bone Valley local fauna.

Table 4.22. Measurements of the tibiotarsi and tarsometatarsi of *Grus canadensis tabida* ($N = 7$, 4 males, 3 females), *Grus canadensis canadensis* ($N = 6$, 3 males, 3 females), and *Grus* species A. from the Love Bone Bed local fauna. Data are mean \pm standard deviation and range. Abbreviations are defined in methods section.

<u>Measurements</u>	<u>G. c. tabida</u>	<u>G. c. canadensis</u>	<u>Grus sp. A</u>
Tibiotarsus			
W-SHAFT	9.46 \pm 0.16 9.2 - 9.6	8.27 \pm 0.88 7.2 - 8.8	9.5
D-SHAFT	8.24 \pm 0.38 7.7 - 8.8	6.97 \pm 0.95 5.9 - 8.4	7.8
W-DIST-CR	18.73 \pm 0.84 17.7 - 20.1	17.33 \pm 2.09 15.2 - 20.3	18.8
W-DIST-CD	14.30 \pm 0.81 12.7 - 15.0	13.05 \pm 1.48 11.5 - 15.1	14.1
D-MCON	18.73 \pm 0.76 17.5 - 19.7	17.52 \pm 2.14 15.1 - 20.6	17.9
D-LCON	18.39 \pm 0.60 17.3 - 19.1	16.80 \pm 1.86 14.7 - 19.6	17.0
D-ICON	10.29 \pm 0.38 9.7 - 10.9	9.32 \pm 0.86 8.3 - 10.4	9.7
Tarsometatarsus			
W-PROX	20.83 \pm 0.99 19.8 - 22.2	19.23 \pm 1.93 17.3 - 21.6	22.5
D-PROX	13.37 \pm 0.33 12.9 - 13.8	11.70 \pm 1.01 10.4 - 13.1	12.7
D-PROX-L	19.57 \pm 0.80 18.5 - 20.5	17.82 \pm 1.59 16.4 - 20.2	19.0

Table 4.23. Measurements of the humeri, tibiotarsi, and tarsometatarsi of *Grus americana* ($N = 9$ maximum, 2 males, 2 females, 5 unsexed), *Grus japonensis* ($N = 6$ maximum, all unsexed), and *Grus* sp. B. from the Love Bone Bed local fauna. Data are mean \pm standard deviation and range. Abbreviations are defined in methods section. (*) Specimen abraded or broken.

<u>Measurements</u>	<u><i>G. americana</i></u>	<u><i>G. japonensis</i></u>	<u><i>Grus</i> sp. B.</u>
Humerus			
W-DIST	35.93 ± 1.84 $34.0 - 38.5$	38.73 ± 1.48 $37.2 - 41.5$	35.7
D-DIST	20.56 ± 1.69 $18.8 - 23.8$	21.13 ± 0.94 $19.8 - 22.3$	18.0; *17.9
Tibiotarsus			
W-SHAFT	11.19 ± 0.81 $10.3 - 13.0$	12.23 ± 0.34 $11.8 - 12.8$	10.7
D-SHAFT	9.79 ± 0.83 $8.6 - 11.3$	10.33 ± 0.45 $9.7 - 11.0$	10.7
W-DIST-CR	22.68 ± 1.00 $21.0 - 24.1$	24.83 ± 0.91 $23.9 - 26.4$	*23.7; 23.9; 23.1
W-DIST-CD	16.97 ± 0.71 $15.8 - 18.1$	18.52 ± 1.11 $17.2 - 20.4$	18.8; *15.2
D-MCON	21.72 ± 1.16 $21.2 - 23.6$	24.93 ± 0.88 $23.5 - 25.6$	*24.1; *21.8; *23.2
D-LCON	21.29 ± 1.33 $19.6 - 23.1$	23.33 ± 0.96 $22.2 - 24.5$	*22.8; 24.0; *21.8; *21.5
D-ICON	12.64 ± 0.62 $11.6 - 13.6$	13.08 ± 0.48 $12.5 - 13.6$	13.04 ± 0.78 (5) $12.3 - 14.2$

Table 4.23--continued

<u>Measurements</u>	<u>G. americana</u>	<u>G. japonensis</u>	<u>Grus sp. B.</u>
<u>Tarsometatarsus</u>			
W-PROX	24.83 \pm 0.93 23.4 - 26.0	26.33 \pm 2.49 21.9 - 28.6	26.36 \pm 0.81 (5) 25.3 - 27.5
D-PROX	16.02 \pm 1.36 14.5 - 17.5	19.8	17.86 \pm 1.25 (5) 15.7 - 18.7
D-PROX-L	23.14 \pm 1.33 22.0 - 24.4	25.7	23.70 \pm 0.62 (5) 23.0 - 24.5
TRII-TRIV	20.47 \pm 1.40 18.1 - 22.5	22.93 \pm 1.23 22.1 - 25.4	19.8; 21.8
TRII-TRIV	20.58 \pm 1.90 17.9 - 22.9	23.62 \pm 0.87 22.3 - 24.9	19.9
W-TRII	6.93 \pm 0.58 6.5 - 8.0	7.95 \pm 0.29 7.6 - 8.4	7.48 \pm 0.35 (4) 7.3 - 8.0
D-TRII	13.60 \pm 0.45 12.8 - 14.0	15.15 \pm 0.56 14.4 - 15.9	*12.2; 13.3; 14.1
W-TRII	9.95 \pm 0.36 9.6 - 10.0	11.33 \pm 0.49 10.9 - 12.2	10.25 \pm 0.44 (4) 9.8 - 10.8
D-TRII	12.33 \pm 0.56 11.5 - 13.0	13.98 \pm 0.59 13.0 - 14.5	13.3; *12.7; 13.4
W-TRIV	6.57 \pm 0.49 6.1 - 7.3	7.52 \pm 0.32 7.1 - 7.9	*6.0; 6.4; 6.6
D-TRIV	14.43 \pm 0.52 13.6 - 15.0	15.65 \pm 0.42 15.1 - 16.2	13.2; *13.4; 14.7

Table 4.24. Measurements of the tibiotarsi of Balearica pavonica (N = 8, 4 males, 4 females) and Balearicinae, genus and species indet. from the Bone Valley Mining District. Data are mean \pm standard deviation and range. Abbreviations are defined in methods section. (*) Specimen abraded or broken.

<u>Measurement</u>	<u>Balearica pavonica</u>	<u>Balearicinae, genus indet.</u>
Tibiotarsus		
W-SHAFT	9.16 \pm 0.49 8.2 - 9.8	8.3
D-SHAFT	7.98 \pm 0.44 7.4 - 8.6	6.6
W-DIST-CR	19.49 \pm 0.80 18.1 - 20.4	15.8
W-DIST-CD	13.10 \pm 0.79 12.2 - 14.4	11.8
D-MCON	19.33 \pm 0.98 17.4 - 20.6	*14.0
D-LCON	18.04 \pm 0.66 17.5 - 19.0	14.1
D-ICON	10.75 \pm 0.45 10.1 - 11.5	8.3
		-

Table 4.25. Measurements of the tarsometatarsi of Aramornis longurio (F:AM 6269, holotype) and Aramornis sp. from the Love Bone Bed local fauna. Abbreviations are defined in methods section. (*) Specimen abraded or broken.

<u>Measurements</u>	<u>Aramornis longurio</u>	<u>Aramornis</u> sp.
Tarsometatarsus		
W-TRII	4.2	4.4
D-TRII	—	*7.2
W-TRIII	5.7	*6.0
D-TRIII	7.2	*7.7

Family Rallidae Vigors, 1825

Family Characters. See references in family remarks section; also Gilbert, et al. (1981).

Material. Love Bone Bed local fauna; UF 26015, UF 29714, UF 29709, UF 25787, coracoid fragments.

Remarks. The above material appears to be rallid, but is not identifiable to the generic level.

Genus Rallus Linnaeus, 1758

Rallus sp. A

Material. Love Bone Bed local fauna; UF 25936, distal end left tarsometatarsus.

Remarks. Near Crex crex in size. Decidely larger than Rallus limicola, but smaller than Rallus longirostris. I have not been able to find qualitative characters in the distal ends of the tarsometatarsus to distinguish between Rallus and Crex and have therefore arbitrarily assigned these specimens to Rallus.

Rallus sp. B

Material. Bone Valley Mining District, Palmetto Mine; UF 21060, humeral end right coracoid. Payne Creek Mine; UF 21204, proximal end left tarsometatarsus.

Remarks. Coracoid slightly smaller than that of females of Rallus longirostris. Agrees with Rallus by having a small procoracoid process. Tarsometatarsus near Crex crex in size, or intermediate between Rallus limicola and Rallus longirostris. These two specimens could possibly represent two different species, but owing to the slight difference in size and the lack of additional specimens, I have listed them together as

representing an undetermined species of Rallus until better material is available.

Rallus (cf.) sp. C.

Material. Love Bone Bed local fauna; UF 25732, distal end left humerus; UF 26025, UF 26027, UF 26030, UF 29705, UF 29712, humeral ends right coracoids; UF 29708, left coracoid; UF 26007, UF 26025, UF 29702, UF 29703, UF 29704, UF 29710, UF 29711, UF 29713, UF 67807, humeral ends left coracoids; UF 29707, distal ends right tarsometatarsus.

Remarks. All specimens badly water-worn, within the size range of Rallus limicola or Porzana carolina or slightly larger. I cannot distinguish between these two genera on the basis of waterworn elements, and have therefore arbitrarily assigned these specimens to Rallus on the basis of size.

Undescribed Genus and Species

Material. Love Bone Bed local fauna; UF 25727, proximal end left humerus; UF 25836, UF 25849, UF 29715, UF 29716, UF 29717, complete (or nearly so) right coracoids; UF 29718, humeral end right coracoid; UF 29719, humeral end left coracoid; UF 25865, UF 25866, distal ends right tarsometatarsi.

McGehee Farm local fauna; UF 9494, proximal end right humerus; UF 29748, nearly complete right coracoid.

Description. Coracoid with a greatly expanded procoracoid process, extending relatively far down shaft; shaft fairly slender; dorsal surface not deeply excavated; coracoid fenestra small; lateral process greatly expanded (Fig. 4.9).

Humerus with shallow pneumatic foramen; wide and deep capital groove. Crest-like margo caudalis extending from distal end of capital groove (Fig. 4.9). Deltoid crest greatly expanded. Tarsometatarsi worn and badly abraded and are assigned here mainly on the basis of size.

Distinguished from all genera examined (listed below) by having the following combination of characters: coracoid with a large procoracoid, flared medially, causing the triosseal canal to be open; dorsal surface of coracoid not deeply excavated. Humerus with large deltoid crest and well-developed capital shaft ridge.

Remarks. In trying to place this fossil material in a genus, I have examined the skeletons of a large number of genera (number of species in parentheses). For convenience, nomenclature follows Peters (1934), but see Olson (1973b) for phylogenetic relationships. Genera examined include: Rallus (6), Alantisia (1), Ortygonax (2), Amaurolimnas (1), Rallina (1), Aramides (3), Gymnocrex (1), Gallirallus (2), Habroptila (1), Himantornis (1), Canirallus (1), Crex (1), Limnocorax (1), Porzana (7), Laterallus (4), Micropygia (1), Coturnicops (1), Neocrex (1), Sarothrura (1), Poliolimnas (1), Porphyriops (1), Tribonyx (1), Amaurornis (1), Gallicrex (1), Gallinula (2), Porphyryula (1), Porphyrio (3), and Fulica (6).

None of the genera above match the characters of the fossil material. There is a superficial resemblance of the coracoid (especially the enlarged procoracoid process) to Canirallus, Gymnocrex, Aramides, and Amaurolimnas. This appears to be due to shared primitive characters between the fossil rail and these primitive living rails (Olson, 1973b).

Additional comparisons with other living and fossil rails are needed to determine the systematic position of this fossil rail. Possibly Fulica infelix Brodkorb, known only from the distal end of a tibiotarsus,

from the late Miocene of Oregon, should be compared further with this undescribed genus and species.

Remarks on the Family Rallidae.

The fossil record of rails has been recently reviewed (Feduccia, 1968; Cracraft, 1973; Olson, 1974b, 1977b; Kurochkin, 1980; and references therein). The generic or higher status of living rails has been reviewed by Olson (1973b) and accounts have appeared for all living species (Ripley, 1977).

The obvious lack of rails from many of the fossil localities in this study is probably size related, whether due to inadequate sampling while collecting, or bone destruction during deposition (or both).

Several fossil species already described should be re-examined as additional material becomes available from Florida. The fossil species Rallus phillipsi Wetmore, 1957, from the Wickieup l. f. of Arizona was described as intermediate in size between Rallus limicola and Rallus longirostris. Olson (1977b) notes that when a larger series of recent comparative skeletons are examined, Rallus phillipsi falls well within the lower size range of the living Rallus longirostris. Rallus sp. A and perhaps Rallus sp. B possibly has affinities with R. phillipsi, but without more material, this cannot be determined.

Rallus prenticei Wetmore 1944 from the Blanca of Kansas and Idaho, was described as being somewhat larger and heavier than the living Rallus limicola. Rallus sp. C may have affinities with this species. Better material is again needed to identify this species with confidence.

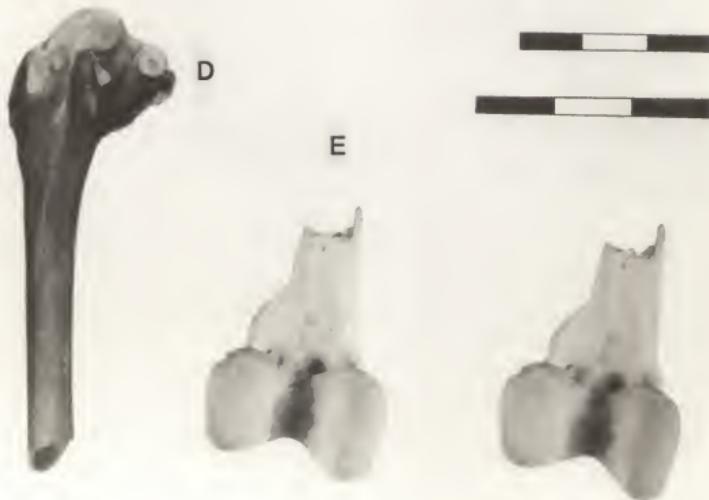
Figure 4.9. A - C. Rallid, undescribed genus. A, B. Right coracoid, UF 29717. A. Ventral view. B. Dorsal view. C. Proximal end right humerus, UF 9494, caudal view. D. Philomachus sp., proximal end left humerus, UF 60062, caudal view. E. Tytonid, undescribed genus, distal end right tibiotarsus, UF 25926, cranial view, stereopair. Scale A - D (top) = 1.5 cm; E (bottom) = 1.5 cm.



A

B

C



D

E

Order Charadriiformes (Huxley, 1867)

Remarks. The phylogenetic position of the Phoenicopteridae has long been debated by avian systematists. Flamingos have been placed with the storks in the Order Ciconiidae, with the ducks in the Order Anseriformes, or commonly in their own order, the Phoenicopteriformes. I follow the recent work by Olson and Feduccia (1980) which establishes the Phoenicopteridae as a family within the Order Charadriiformes, as shown by their life history, behavior, myology, pterylosis, natal down, oology, parasites, biochemistry, osteology, and paleontology.

Family Phoenicopteridae Bonaparte, 1831

Remarks. Recent flamingos are usually divided into three genera, based primarily on bill morphology and the presence (or absence) of a very reduced hind toe. Phoenicopterus is usually considered to have the most primitive feeding apparatus of the three, with Phoenicoparrus and Phoeniconaias being more specialized. There are no characters in the post-cranial skeleton which will define these genera (Olson and Feduccia, 1980; personal observation). For the basis of comparison with fossil species, I consider the living species to be congeneric. Olson and Feduccia (1980) also consider the fossil genera Gervaisia Harrison and Walker and Harrisonavis Kashin to be junior synonyms of Phoenicopterus Linnaeus. Additionally, I consider Leakeyornis Rich and Walker to also be a junior synonym of Phoenicopterus, as even the original authors of Leakeyornis suggest (Rich and Walker, 1983: 104)! I follow Olson and Feduccia (1980) and A. H. Miller (1944) in not recognizing the Palaelodidae as a separate family. Both Palaelodus and Megapalaelodus may be separated from Phoenicopterus by having a shorter tibiotarsus and a shorter and more laterally compressed tarsometatarsus (Olson, ms.).

These two genera are thought to be more specialized for swimming than Phoenicopterus.

Genus Phoenicopterus Linnaeus, 1758

Remarks. The post-cranial skeletal elements of flamingos exhibit an extremely large amount of sexual and individual variation. This variability is especially evident in the tibiotarsus and tarsometatarsus, with the males typically being much larger than females. The C. V.'s of measurements from the Bone Valley material do not exceed those of a Recent species, suggesting a single species is present here. At the Love Bone Bed specimens range in size from smaller than that of the modern P. minor to larger than that of the modern P. ruber, indicating that more than one species is present. In trying to separate the Love Bone Bed specimens into species, I found I could only separate the two extremes of this continuum. I have noted these extremes in the referred material as "large" or "small".

Material. Love Bone Bed local fauna; UF 29678, humeral end left coracoid; UF 26088, proximal end left radius; UF 29677, distal end right ulna; UF 25769, proximal end left femur; UF 25957, distal portion of shaft of tarsometatarsus; UF 25943, UF 25930, distal fragments left tarsometatarsus; UF 26031, UF 26035, UF 26042, UF 26043, pedal phalanges.

Remarks. The material listed above is considered to be either too abraded or too undiagnostic for a more refined taxonomic assignment.

Phoenicopterus floridanus Brodkorb, 1953

Material. Bone Valley Mining District, Palmetto Mine (= Locality 2 of Brodkorb, 1955), referred by Brodkorb; PB 147, distal end right tibiotarsus (Holotype, not seen), PB 202, shaft right tibiotarsus (=

"paratype"), PB 146, PB 300, distal ends right tarsometatarsi (= "paratype"). New material (referred by Becker); PB 139, proximal end right carpometacarpus; PB 7980, distal end left tibiotarsus. Nichols Mine; UF 24623, distal end right tibiotarsus (tentatively referred); Ft. Green Mine (# 13 dragline), UF 52422, distal end right tibiotarsus; Payne Creek Mine, UF 67811, distal end right tibiotarsus; No Specific Locality; UF 29743, distal end right tibiotarsus; Palmetto Mine; UF 21164, distal end right tarsometatarsus.

Description/ Remarks. For qualitative characters and remarks see Brodkorb (1953b, 1955a). Measurements given in Table 4.26.

Phoenicopterus sp. A

Material. Love Bone Bed local fauna; UF 25905, UF 25907, UF 29685, UF 29744, distal ends right tibiotarsi (large); UF 25882, UF 25883, UF 25892, UF 25898, UF 25910, UF 29684, distal ends left tibiotarsi (large); UF 29686, distal end right tibiotarsus (small); UF 25889, UF 25899, UF 25927; distal ends left tibiotarsi (small); UF 25881, UF 25897, distal ends right tibiotarsi (abraded); UF 25895, UF 29682, UF 29683, distal ends left tibiotarsi (abraded); UF 29679, proximal end right tarsometatarsus; UF 25859, UF 25864, distal ends right tarsometatarsi; UF 25932, UF 25935, UF 29680, UF 29681, distal ends left tarsometatarsi.

McGehee Farm local fauna; UF 11103, distal end right tarsometatarsus.

Description. Tibiotarsi with a pronounced bimodal size distribution, less so in the tarsometatarsi. The group of small tibiotarsi cannot be distinguished from the tibiotarsi of P. floridanus when specimens are directly compared. The group of large tarsometatarsi

may be distinguished from that of P. floridanus by (1) larger size, (2) proportionally wider distal end, (3) more robust shaft, (4) papilla just medial to the proximal opening of the tendinal canal more expanded.

Comparisons of the distal end of a right tibiotarsus (USNM 242202) from the Lee Creek local fauna with the large subset of tarsometatarsi from the Love Bone Bed show it to be similar in all characters except for the notch on the distal surface of the external condyle being slightly more pronounced in distal end view. Distal opening of the tendinal canal more transversely elongated and nutrient canal lateral to papilla is larger and more pronounced in the Love Bone Bed specimens than in the Lee Creek specimen in cranial view. Groove usually deeper and more pronounced in the Love Bone Bed specimens than in the one from Lee Creek in lateral view. In caudal view, the most cranial portion of the lateral edge of the articular surface is expanded cranially and laterally in Lee Creek specimens and not in specimens from the Love Bone Bed.

Distal ends of tarsometatarsi from the Love Bone Bed and McGehee may be distinguished from the distal ends of tarsometatarsi of P. floridanus by (1) averaging larger and more robust (P. floridanus smaller and more gracile) (2) caudal portion of the articular surface of trochlea III is raised above shaft (P. floridanus blends relatively smoothly with shaft) (3) Distal foramen elliptical and larger (P. floridanus smaller, more nearly circular) (4) Prominent nutrient foramen pierces the caudal surface of the shaft cranial to the distal foramen (P. floridanus nutrient foramina very small or absent).

Remarks. The flamingos from the Love Bone Bed show a distinct bimodal distribution in the size classes of the tibiotarsi, with the smaller group of tibiotarsi being very similar, if not identical with,

that of P. floridanus. Along with these small specimens are a group of larger specimens which represent a much larger flamingo. If this variation is considered to be sexual in origin, then there is more size variation than has ever been observed in any single living or fossil species of flamingo. This suggests that there are two species of flamingos present at the Love Bone Bed, which overlap in size. The similarity of the smaller flamingo from the Love Bone Bed to that of P. floridanus from the Bone Valley (4 MA later in time) suggest that flamingos have had a slow evolutionary rate. Pending further studies on other Miocene flamingos, particularly P. stocki, I have left these Florida specimens unassigned to species.

Remarks on the Family Phoenicopteridae.

Fossil species of Phoenicopterus are now known from the Aquitanian in Europe and the late Miocene to the late Pleistocene of North America. Phoenicopterus croizeti Gervais, was described from the Aquitanian of France. It is known from abundant material and has recently been restudied (Cheneval, 1984). Phoenicopterus stocki Miller, is based on a distal tibiotarsus from the Hemphillian Yepomera local fauna. It is said to have the morphological characters of the genus, but is of pigmy size (Miller, 1944: 77). Phoenicopterus floridanus Brodkorb, is discussed above. Other Neogene species of Phoenicopterus include only P. novaehollandiae A. Miller, from the late Oligocene or early Miocene of Australia. Pleistocene species of Phoenicopterus include P. copei Shufeldt, from Fossil Lake in Oregon and Manix Lake in California and P. minutus from Manix Lake in California. All North American fossil species should be revised and analysed with a larger database of skeletons to account adequately for the large size variation present.

Table 4.26. Measurements of the tibiotarsi and tarsometatarsi of the fossil species Phoenicopterus floridanus from the Bone Valley Mining District, Phoenicopterus sp. A. (large), and Phoenicopterus sp. B. (small) from the Love Bone Bed local fauna. Data are mean \pm standard deviation (number) and range. Abbreviations defined in the methods section.

<u>Measurement</u>	<u>P. floridanus</u>	<u>P. sp. A (lg.)</u>	<u>P. sp. A (sm.)</u>
Tibiotarsus			
W-DIST-CR	15.09 ± 0.41 (4) $14.5 - 15.4$	17.53 ± 0.70 (8) $16.3 - 18.2$	15.0; 15.8
W-DIST-CD	10.39 ± 0.55 (4) $9.9 - 11.0$	12.23 ± 0.33 (8) $11.8 - 12.8$	9.6; 11.1
D-MCON	17.49 ± 0.81 (4) $16.4 - 18.3$	20.33 ± 0.58 (6) $19.3 - 20.8$	16.8; 19.5
D-LCON	17.51 ± 0.74 (5) $16.8 - 18.5$	20.32 ± 0.63 (7) $19.5 - 21.5$	16.8; 19.1
Tarsometatarsus			
W-TRIII	7.83 ± 0.64 (3) $7.1 - 8.3$	8.08 ± 0.60 (5) $7.1 - 8.6$	Combined in column to the left
TRIII-TRIV	8.3; 9.4	14.25 ± 0.24 (4) $14.1 - 14.6$	
TRII-TRIV	13.4; 15.0	15.60 ± 0.35 (3) $15.4 - 16.0$	-

Table 4.27. Measurements of the tibiotarsii and tarsometatarsi of the Recent *Phoenicopterus jamesi* (N = 9, 1 male, 2 females, 6 unsexed), *Phoenicopterus chilensis* (N = 8, 3 males 2 females, 3 unsexed), *Phoenicopterus ruber* (N = 15, 6 males, 7 females, 2 unsexed), and *Phoenicopterus minor* (N = 7, 3 males, 4 females). Data are mean \pm standard deviation (number) and range. Abbreviations defined in the methods section.

Measurement	<i>P. jamesi</i>	<i>P. chilensis</i>	<i>P. ruber</i>	<i>P. minor</i>
Tibiotarsus				
W-DIST-CR	14.49 \pm 0.67 13.6 - 15.4	14.96 \pm 0.65 14.2 - 16.3	15.70 \pm 0.87 14.6 - 17.2	12.79 \pm 0.65 12.0 - 13.6
W-DIST-CD	10.21 \pm 0.39 9.6 - 10.8	10.26 \pm 0.65 9.5 - 11.7	10.93 \pm 0.70 9.8 - 12.2	8.85 \pm 0.46 8.0 - 9.3
D-MCON	15.79 \pm 0.87 14.3 - 16.8	16.17 \pm 0.64 15.4 - 17.4	18.70 \pm 1.15 16.3 - 20.8	14.33 \pm 0.67 13.2 - 15.1
D-LCOT	15.29 \pm 0.69 13.9 - 16.3	16.29 \pm 0.53 15.5 - 17.1	18.80 \pm 1.19 16.6 - 21.2	14.23 \pm 0.68 13.1 - 15.0
Tarsometatarsus				
W-TRIIII	7.09 \pm 0.44 6.3 - 7.7	7.55 \pm 0.38 7.2 - 8.4	7.85 \pm 0.50 7.2 - 8.8	6.31 \pm 0.40 5.7 - 6.8
TRIIII-TRIV	11.92 \pm 0.49 11.2 - 12.5	12.47 \pm 0.37 11.9 - 13.1	13.91 \pm 0.86 12.6 - 15.9	11.15 \pm 0.65 10.3 - 12.0
TRIIII-TRIV	14.01 \pm 0.64 13.2 - 15.0	14.13 \pm 0.97 13.0 - 15.9	14.99 \pm 0.80 13.7 - 16.5	12.22 \pm 0.77 11.6 - 13.5

Family Jacanidae (Stejneger, 1885)

Characters. The Jacanidae may be distinguished from other families in this order by having a tarsometatarsus with an extremely large distal foramen with a deep tendinal groove leading into it and a deep pit present on the medial surface of the inner trochlea (Olson, 1976). Coracoid with procoracoid not perforated by a coracoidal fenestra (perforated in all Charadriform families except the Rostratulidae, Scolopacidae, Thinocoracidae, and Pedionomidae). Elongated tuberosity (for attachment of part of the membrana sternocoracoclavicularis) present on the procoracid and well developed in Jacanidae (less developed in the Rostratulidae, small but distinct in Pedionomus; lacking in other charadriforms).

Genus Jacana Brisson, 1760

Jacana farrandi Olson, 1976

Material. McGehee Farm local fauna (referred by Olson, 1976); UF 21219 (holotype), distal end of left tarsometatarsus, missing trochlea IV; UF 11108 (paratype), left coracoid.

Love Bone Bed local fauna (referred by Becker); UF 25824, UF 29694, UF 29696, UF 29698, humeral ends left coracoids; UF 26016, UF 26026, UF 29690, UF 29691, humeral ends right coracoids; UF 29700, extreme proximal end right humerus (tentatively referred); UF 25728, proximal end of left humerus; UF 67806, distal end left tibiotarsus.

Description/ Remarks. Proximal end and shaft of humerus (UF 25728) differs from Jacana spinosa by having shaft more gracile, pneumatic fossa less deep, head of humerus not undercut by capital groove, and the small papilla-like process not present. Deltoid crest broken. Coracoid similar to the paratype coracoid described by Olson (1976). The

coracoids range in size from similar to the paratype of Jacana farrandi to decidedly larger. This supports Olson's assertion (1976:261-262) that the paratype of J. farrandi (UF 11108) is from a male. Tibiotarsus similar to Jacana spinosa except for a reduced lateral epicondyle. For type description and additional remarks see Olson (1976).

Remarks on the Family Jacanidae.

Rhegminornis calobates was originally described by Wetmore (1943b) as a jacana from the early Hemingfordian Thomas Farm local fauna. Olson and Farrand (1974) and later Steadman (1980) showed that this species has affinities with the Phasianidae (Meleagridinae). Olson (1976) later described the only fossil species of this family now known, Jacana farrandi (discussed above).

The Jacanidae have long been allied with the Rostratulidae of South America. In these two families, the females are larger than the males and the young are similar (downy, strongly marked dorsally with black-edged stripes from the forehead to tail). The similar osteology of these two families support their association. Strauch (1978) presented a subordinal classification of the Charadriiformes and associated the Jacanidae, Rostratulidae, Scolopacidae, Phalaropodidae, and Thinocoridae in his suborder Scolopaci. Characters used to support this classification included the absence of the maxillo-palatine strut A, absence of the coracoidal fenestra, and presence of a ridge in the capital groove of the humerus. Olson and Steadman (1981) showed that Pedionomus (Pedionomidae) was not only a Charadriiform, but had affinities with at least one of these families (Thinocoracidae). The relationships of these families need additional study.

Table 4.28. Measurements of the humeri and tibiotarsi of *Jacana spinosa* ($N = 12$, 6 males, 6 females) and *Jacana farrandi*. For measurements of the type (tarsometatarsus) and paratype (coracoid) see Olson (1976). Data are mean \pm standard deviation and range. Abbreviations are defined in the methods section.

<u>Measurements</u>	<u><i>J. spinosa</i></u>	<u><i>J. farrandi</i></u>	
	<u>males</u>	<u>females</u>	
Humerus			
W-SHAFT	2.67 ± 0.05 $2.6 - 2.7$	3.10 ± 0.13 $3.0 - 3.3$	3.4
D-SHAFT	2.25 ± 0.08 $2.1 - 2.3$	2.70 ± 0.09 $2.6 - 2.8$	2.9
W-PROX	8.25 ± 0.23 $7.9 - 8.4$	9.70 ± 0.52 $9.0 - 10.6$	9.6
D-PROX	4.68 ± 0.12 $4.5 - 4.8$	5.48 ± 0.18 $5.2 - 5.7$	5.9
D-HEAD	2.45 ± 0.08 $2.4 - 2.6$	2.82 ± 0.08 $2.7 - 2.9$	3.0
Tibiotarsus			
W-SHAFT	2.33 ± 0.10 $2.2 - 2.5$	2.67 ± 0.14 $2.5 - 2.8$	2.8
D-SHAFT	1.93 ± 0.08 $1.8 - 2.0$	2.25 ± 0.14 $2.1 - 2.4$	2.6
W-DIST-CR	4.70 ± 0.11 $4.5 - 4.8$	5.35 ± 0.08 $5.3 - 5.5$	5.6
W-DIST-CD	3.52 ± 0.12 $3.4 - 3.7$	3.92 ± 0.04 $3.9 - 4.0$	3.9
D-MCON	5.28 ± 0.17 $5.1 - 5.5$	5.70 ± 0.20 $5.4 - 5.9$	5.8
D-LCON	4.90 ± 0.13 $4.7 - 5.0$	5.37 ± 0.10 $5.2 - 5.5$	5.6
D-ICON	3.32 ± 0.18 $3.1 - 3.6$	3.50 ± 0.14 $3.3 - 3.7$	3.7

Family Scolopacidae Vigors, 1825

Remarks. Many of the specimens discussed below have been arbitrarily assigned to the genus Calidris because of their similarity in size and overall morphology to this genus. I have been unable to find generic characters (i. e. non-size related) on the elements here preserved which will confidently separate Calidris from other genera of scolopacids. Possibly with study of additional series of all scolopacid genera, characters could be isolated. But for the present, the following generic assignments should be regarded as tentative.

Brodkorb (1955a, 1963a, 1967) described four species of scolopacids from the late Miocene and early Pliocene of Florida--Calidris pacis, Erolia penepusilla, and Limosa ossivallis from the Bone Valley Mining District and Ereunetes rayi from the McGehee Farm local fauna. They are listed below for the sake of completeness, but additional specimens usually have not been assigned to them, pending further comparisons with living and fossil species. All specimens are assigned at the species level on the basis of size. This approach has the effect of overestimating the diversity of scolopacids now known from the late Miocene and early Pliocene of Florida.

Genus Limosa Brisson, 1760Limosa ossivallis Brodkorb, 1967

Material. Bone Valley Mining District, near Brewster (referred by Brodkorb, 1955a); PB 526, distal end right tibiotarsus (holotype); PB 527 proximal end right tibiotarsus ("paratype"). Specimens referred by Becker: Bone Valley Mining District, specific locality unknown; UF 60817, distal end left humerus; UF 61597, left coracoid; UF 61600,

proximal end right tarsometatarsus; Palmetto Mine; UF 21092, distal end right tibiotarsus.

Remarks. Assignment of additional specimens to Limosa ossivallis very tentative as most of the skeletal elements are abraded. These skeletal elements represent a scolopacid of the correct size for this species (see Brodkorb, 1955a for measurements). The type material, and the material referred above, should be compared with Limosa vanrossemi L. Miller, which was described from the Lompoc local fauna of Mohinian age (=late Miocene) of California. Miller (1925) states that it is closest to the living Limosa fedoa and shows but slight divergence.

Genus Erolia Vieillot, 1816

Erolia penepusilla Brodkorb, 1955

Material. Bone Valley Mining District, near Brewster; PB 611, distal end left humerus (holotype).

Remarks. Brodkorb (1955a) found this species to be larger than Erolia temminckii, E. ruficollis, E. minutilla, Ereunetes pusillus, and Ereunetes mauri; smaller than Erolia bairdii and E. fuscicollis. E. penepusilla appears to be closest to E. minutilla.

Genus Ereunetes Illiger, 1811

Ereunetes rayi Brodkorb, 1963

Material. McGehee Farm local fauna; UF 3978, humeral end left coracoid (holotype).

Remarks. Brodkorb (1963a) found this species to be larger than that of Ereunetes pusillus, E. mauri, and Erolia minutilla; but smaller than Erolia bairdii and E. fuscicollis. Ereunetes rayi falls within the same

size class as Erolia penepusilla (above) and should be further compared with this species.

Genus Calidris Merrem, 1804

Calidris pacis Brodkorb, 1963

Material. Bone Valley Mining District, near Brewster; PB 594, proximal end left humerus (Holotype).

Remarks. Brodkorb (1955a) states this species is almost identical in size to Calidris canutus (see Brodkorb, 1955a:22 for measurements), but differs significantly in the characters of the proximal end of the humerus. Brodkorb (1955a:22) further suggests that this species may require generic separation from Calidris when additional material is known.

"Calidris" sp. 1

Material. Love Bone Bed local fauna; UF 25807, UF 29697, humeral ends left coracoids; UF 26008, right coracoid; UF 29692, humeral end right coracoid.

McGehee Farm local fauna; UF 3978, humeral end left coracoid; UF 9487, right coracoid.

Bone Valley Mining District, Ft. Green Mine (# 13 dragline); UF 53944, right humerus lacking distal end.

Remarks. Skeletal elements similar in size to those of Calidris minutilla, C. minuta, C. pusilla, and C. mauri. Slightly smaller than those of C. subminuta females, C. ruficollis, C. bairdi, and C. fusicollis; slightly larger than that of C. temminckii females.

"Calidris" sp. 2

Material. Love Bone Bed local fauna, UF 26018, right coracoid.

Remarks. Coracoid similar in size to that of Calidris melanotos and morphologically indistinguishable.

"Calidris" sp. 3

Material. McGehee Farm local fauna; UF 31776, distal end left tarsometatarsus.

Remarks. Distal tarsometatarsus larger than that of Calidris minutilla and C. ruficollis; smaller than that of C. fusicollis.

Specimen very tentatively referred to genus.

Genus indet. sp. 4

Material. Love Bone Bed local fauna, UF 25760, right carpometacarpus missing minor metacarpus.

Remarks. Carpometacarpus similar to that of Calidris minutilla.

Genus Actitis Illiger, 1811??Actitis sp. indet. sp 5

Material. Love Bone Bed local fauna, UF 29701, distal end right tibiotarsus.

Remarks. Tibiotarsus is about the size of, and very similar in morphology to Actitis macularia. Species 3 above may belong here.

Assignment to Actitis very tentative.

Genus Arenaria Brisson, 1760??Arenaria sp. indet. sp. 6

Material. Love Bone Bed local fauna, UF 25814, UF 29693, humeral ends left coracoids.

Remarks. The fossil coracoids are very similar in size and morphology to the males of Arenaria melanocephala, but are slightly more robust. Assignment to genus very tentative.

Genus indet. sp. 7

Material. Love Bone Bed local fauna, UF 25871, distal end left tibiotarsus; UF 25858, distal end right tarsometatarsus.

Remarks. Fossil skeletal elements similar to those of females of Limosa fedoa. Brief comparisons with Limosa ossivallis shows the tibiotarsus from the Love Bone Bed local fauna to have a smaller transverse width of both the shaft and the anterior portion of the distal end and is of a slightly smaller size. Additional comparisons are needed with Limosa vanrossemi from the Miocene of California.

Genus indet. sp. 8

Material. Love Bone Bed local fauna, UF 25820, UF 25822, UF 29695, UF 29699, left coracoids, broken and abraded; UF 26009, UF 26013, UF 26028, UF 29867, UF 29688, UF 29689, right coracoids, broken and abraded.

Remarks. Coracoids similar in size to that of females of Tringa flavipes, but slightly more slender. As all coracoids are broken or abraded to varying degrees, assignment to genus is unwarranted.

Genus Philomachus Merrem, 1804

?Philomachus sp.

Material. Bone Valley Mining District, Ft. Green Mine; UF 60062, proximal end left humerus.

Remarks. After an extended survey of scolopacid genera, I have found this humerus (Figure 4.9) from Ft. Green to be most similar to that of males of Philomachus pugnax. Because Philomachus is only a casual

visitor to North America today and has never been noted from Florida, I hesitate to report it as a fossil until I make additional comparisons with other recent and fossil species; and can distinguish the proximal humerus of all genera of scolopacids with certainty by a differential diagnosis.

Remarks on the Family Scolopacidae.

There are some 20 fossil species of scolopacids, many of which are in need of revision. Reference to these may be found in Olson (ms) and Brodkorb (1967). Living species are treated in Johnsgard (1981).

Order Strigiformes (Wagler, 1830)

Ordinal Characters. Tibiotarsus without tendinal bridge, with ligamental tubercle, condyles prominent, nearly parallel, equal in size, and circular in lateral view (the Psittacidae, the only other New World family with a tibiotarsus lacking a tendinal bridge, does not have condyles which are parallel, equal in size and circular in side view).

Family Tytonidae Ridgway, 1914

Characters. In cranial view, tendinal furrow not excavated (deeply excavated in Strigidae); in caudal view, shaft merges with posterior intercondylar sulcus evenly (depression present slightly craniad in Strigidae).

Tytonidae, undescribed genus

Material. Love Bone Bed local fauna. UF 25926, distal end right tibiotarsus.

Description. Tibiotarsus (Fig. 4.9) distinguished from all species of Tyto examined (T. alba, glaucops, capensis, sanctialbani, ostologa, pollens) and Phodilus badius by having a wider anterior intercondylar sulcus, with the medial condyle sloping gradually into the anterior intercondylar sulcus, and by having the area intercondylaris much broader and more shallow (best seen in anterior view of distal end).

Measurements given in Table 4.29.

Remarks. Although the above specimen is slightly abraded and is a solitary specimen, there is no question that it represents a genus distinct from the two living genera of this family. Additional comparisons with owls from the early Tertiary are needed to determine the exact systematic position of this taxon.

Remarks on the Family Tytonidae

There have been many fossil species of Tyto described (listed in Brodkorb, 1971; Olson, in press); based mainly on size differences. The morphology of the distal end of the tibiotarsus of these fossil species (T. sanctialbani, T. ostologa, and T. pollens examined) is remarkably uniform within this genus and is also very similar to that of Pholidus badius.

There is only one fossil tytonid genus now known. Prosybris Brodkorb is based on the type species P. antiqua (Milne-Edwards, 1863) from the Aquitanian of St.-Gérand-le-Puy, France. It was described on an tarsometatarsus and is not directly comparable with the above specimen from the Love Bone Bed local fauna. The tibiotarsus of Prosybris is unknown.

A number of undescribed Oligocene owls are known. The above specimen should be compared with these before allocating the Love Bone Bed owl to a genus.

Table 4, 29. Measurements of the tibiotarsi of the following tytonid owls: Tyto albus pratincola ($N = 16$, 8 males, 8 females), Tyto glaucopterus ($N = 6$, 2 males, 1 female, 3 unsexed), Tyto capensis ($N = 1$, unsexed), Phodilus badius ($N = 2$, 1 male, 1 unsexed), and tytonid, undescribed species from the Love Bone Bed local fauna. Data are mean + standard deviation and range. Abbreviations defined in the methods section.

<u>Measurements</u>	<u>T. a. pratincola</u>	<u>T. glaucopterus</u>	<u>T. capensis</u>	<u>P. badius</u>	<u>LOV</u>
W-DIST-CR	10.92 + 0.40 10.0 - 11.7	10.18 + 0.53 9.6 - 10.7	10.0	9.6; 9.2	11.7
D-ICON	4.83 + 0.26 4.5 - 5.5	4.47 + 0.48 4.0 - 5.3	4.5	3.5; 3.8	5.3

Family Strigidae Vigors, 1825

Remarks. Femur referable to the Strigidae by having a smooth antero-dorsal condyle slope and having the postero-dorsal portion of the external condyle joining the shaft abruptly (Ford, 1967).

Subfamily Buboninae Vigors, 1815Genus Bubo Dumeéril, 1806(cf.) Bubo sp.

Material. Bone Valley Mining District, Tiger Bay Mine. UF 29782, distal end left femur.

Remarks. Distal end of the femur intermediate in size between that of males and females of Bubo virginianus. Agrees with Bubo (and differs from Strix and Asio) in placement of muscle scars, especially those above the lateral condyle. Differs from Bubo virginianus and Nyctea scandica by having the posterio-medial portion of the medial condyle merging smoothly with the posterior intercondylar sulcus. In other Bubonini examined, the posterior-medial portion of the medial condyle sharply overhangs the popliteal fossa.

Remarks on the Family Strigidae.

There is several undescribed strigids awaiting a comprehensive review. Olson (in press) briefly discusses much of this material.

Order Passeriformes (Linnaeus, 1758)

Ordinal Characters. Coracoids separate, lacking coracoidal fenestra; process small; brachial tuberosity elongate and expanded toward sternal end of element; head of coracoid usually small, somewhat pointed.

Family Fringillidae Vigors, 1825

Genus Palaeostruthus Wetmore, 1925

Palaeostruthus eurius Brodkorb, 1963

Material. Haile VI local fauna; PB 8502, distal portion of left tarsometatarsus (holotype).

Remarks. See Brodkorb (1963a) and Steadman (1981) for discussion and remarks pertaining to this species.

Family Indeterminable

Material. Love Bone Bed local fauna: UF 25806, left coracoid; UF 25772, distal left femur; UF 29727, 29728, humeral ends right coracoids; UF 29729, 29730, humeral ends left coracoids.

Remarks. The above specimens represent a minimum of two species based on size. I have been unable to find characters on the humeral ends of the coracoid to identify these specimens beyond the level of order. Characters given by Hamon (1964) do not characterize the suborders of passerines, although these characters appear adequate to discriminate between the late Pleistocene and Recent taxa of North America which he examined. The difficulties in identifying passerines are due to the large number of genera and the general similarity of morphology within the order (Fürbringer, 1888). This is additionally complicated by the poorly understood interrelationships between genera and families (Olson, ms.).

Remarks on the Order Passeriformes

There have been very few fossil species of passerines described (Brodkorb, 1978). With a few exceptions, still fewer are believably assigned to a genus or family. Most fossil species were compared to very few other species and were not adequately diagnosed as a member of the family in which they were placed.

Nine fossil genera of passerines have been described (Brodkorb, 1978). Miocitta Brodkorb is known only from the late Barstovian Kennesaw local fauna, Colorado. Protocitta Brodkorb is from the Blancan of Texas and Kansas and from the Pleistocene of Florida and Texas. Henocitta Holman was described from the Pleistocene of Florida. All of the above genera were described as medium to large sized jays.

Palaeoscincus Howard, from Mohanian of Tepsquet Creek, California, was described from a slab and represents an extinct family of passerines. Howard (1957) states this family has its affinities with the - Pycnonotidae, Bombycillidae, Corvidae, and Cinclidae.

Necropsar Slater is based on a postcranial skeleton from the Holocene of Rodriguez Island. It is placed in the family Sturnidae.

Genera of fossil icterids include Cremaster Brodkorb from the Pleistocene of Florida, Pandanaris A. H. Miller from the Pleistocene of Florida and California, and Pyelorhamphus A. H. Miller from the Quaternary of New Mexico.

Palaeostruthus Wetmore was described as a late Clarendonian to early Hemphillian genus of emberzid finch from Florida and Kansas. Steadman (1981) synonymized this genus with the living genus Ammodramus. Additionally, Passerina (cf.) is reported from the Hemphillian Yopomera local fauna (Steadman and McKittrick, 1982). These last two genera are

the only reports of nine-primeried oscines in the Tertiary (Steadman and McKittrick, 1982).

No fossil passeriformes are recorded before the Miocene (Brodkorb, 1978; Olson and Feduccia, 1979). This could be explained simply as a sampling bias, but considering the amount of detailed paleontological field work done both in North America and in Europe, this absence seems real, at least on these two continents. Prior the Miocene, a great diversity of small non-passeriforms (mainly Coraciiformes) are known and they evidently occupied many of the niches which are now filled by passerines (Mourer-Chauvire, 1982; Olson and Feduccia, 1979; Feduccia and Olson, 1982). Feduccia and Olson (1982) noting the great radiation of suboscines in South America, speculate that they were present in South America for most of the Tertiary. They also argue that, in addition to the suboscines, the entire order Passeriformes is of South American origin.

CHAPTER V
PALEOECOLOGY

Introduction

In some situations, the avian specimens from one locality could be used to reconstruct the fossil avian communities, and the fossil environments sampled, using methods similar to those of mammalian paleoecologists (see Shipman, 1981). Each locality could then be quantitatively compared to other such fossil localities in North America throughout the latter half of the Cenozoic. Two insurmountable problems, sample size and collection technique, prevent such an approach being applied to the localities included in this study.

Localities from which there are relatively few fossils are not suited, or are severely limited in usefulness, for quantitative paleoecological analyses because necessary data were never recorded and because small forms are often poorly represented (Wolff, 1975). He showed that when collected in a random manner, approximately 12,000 - 25,000 specimens are needed to represent all members of a mammalian community, and that about 500 identifiable specimens are needed just to represent the common members of a community. There is no reason to believe that avian communities can be adequately represented by fewer specimens, certainly when avian communities are as diverse and complex, if not more so, than mammalian communities. Simply put, avian communities cannot be reconstructed definitively from a meager handful of haphazardly collected fossil bird bones. The problem of sample size applies to all local faunas included in this study except for two--the

Love Bone Bed and Bone Valley. Although these two localities have large samples of fossil birds, the techniques used to collect the fossil vertebrates prevent a quantitative paleoecological analysis. Hence I am limited to qualitative statements about the paleoecology of each of the local faunas considered in this investigation. These statements are based primarily on the birds present, the habitats used by their Recent congeners (Blake, 1977; Palmer, 1962, 1975, 1976; Terres, 1980), and on a general knowledge of the geology of the locality and its vertebrate fauna. In general, the paleoecological reconstructions based on fossil birds are similar to those based on other fossil groups.

Local Faunas

Love Bone Bed local fauna. The avifauna of the Love Bone Bed is richly aquatic, with but a minor influence of more terrestrial species. Taxa presently identified include 2 species of grebe, a species of cormorant and one of anhinga, 3 species of heron, 2 species of stork, 2 ibises, one vulture, one osprey, 2 accipitrids, 4 species of geese, 4 species of duck, a turkey, 3 cranes, 3 rails, 2 flamingos, a jacana, 7 species of shorebirds, a barn owl, and 2 species of passerine.

The more abundant species of those listed above include the grebe, Tachybaptus sp.; a tree-duck, Dendrocygna sp.; a tiny species of teal, Anas sp. A.; a larger duck, Anas near A. acuta; a crane, Grus sp. B.; two species of rail, one a species of Rallus cf. sp. C., and the other an undescribed genus; 2 flamingos in the genus Phoenicopterus; a jacana, Jacana farrandi; and a indeterminate genus and species of scolopacid.

These abundant taxa suggest that more than one type of habitat has been sampled. Modern species of grebe typically occur in freshwater, from lakes to shallow ponds. Jacanas occur in freshwater marshes to

shores of rivers and often in ponds with floating vegetation. Species of Dendrocygna may also be found in shallow ponds with floating vegetation, but they have a greater tolerance to brackish water. Scolopacids may be found in grassy marshes, mudflats, estuaries, and edges of ponds. Flamingos are found in shallow water to mudflats. It would seem likely therefore, that the environments around the Love Bone Bed during the time of deposition would include freshwater ponds and streams, but probably also with wet marshes, streams, estuaries, and mudflats nearby.

Although the avifauna from the Love Bone Bed is substantial, the usefulness of this collection for qualitative paleoecological analysis is limited by collection techniques. As in most fossil vertebrate localities, this site was excavated to maximize the number of mammalian specimens recovered per unit time spent digging. While sediment samples were screenwashed for small specimens, it was not done in a systematic fashion. By using these methods, many of the smaller specimens apparently were never collected. In the original study, only two one-quarter cubic meter samples were collected for paleoecological analysis (Webb et al. 1981: 553ff). Each of these small samples was from a different stratigraphic unit; vertebrate remains were reported by weight only with no indication of number of specimens given, or of the weight of the sediment.

It should also be noted that the MNI (minimum number of individuals) of birds as given by Webb et al. 1981: 538) based on preliminary identifications is not MNI but rather the estimated number of species of birds. Neither MNI nor number of specimens are valid indicators of abundance when samples are strongly biased toward larger specimens. It

seems likely that birds with large limb bones (flamingos, cranes) are better represented in the collections than really existed either in the deposit or in the fossil community preserved.

Mixson Bone Bed local fauna. Avian taxa now known from here include two species of grebe (Rollandia sp. and Podilymbus sp. A); a large stork, Ciconia sp. B; unstudied specimens of a large crane (?Grus sp. B), and an anhinga, Anhinga grandis. These taxa suggest a shallow freshwater environment with emergent vegetation surrounded by marshes or "wet prairies". The lack of other avian species, and the lack of a greater number of specimens should not be considered significant. This locality was excavated primarily for the remains of large mammals and only a few specimens of small vertebrates exist in collections.

McGehee Farm local fauna. Avian taxa known from the McGehee Farm l. f. include 2 species of grebe (Rollandia sp. and Tachybaptus sp.); an undetermined species of cormorant; the anhinga, Anhinga grandis; the night-heron, Nycticorax fidens; 2 species of duck, a small species of teal and the other near Anas acuta in size; an undescribed genus of rail; a flamingo, Phoenicopterus sp.; a jacana, Jacana farrandi; and three shorebirds, probably all in the genus Calidris. None are abundant, but the cormorant and the ducks are the most common. Based on the occurrence of a similar set of avian taxa, the environments surrounding McGehee Farm during deposition were probably very similar to those at the Love Bone Bed.

Withlacoochee River 4A local fauna. Only two avian species have been recovered from this Hemphillian site. They consist of a single femur representing an indeterminate species of Buteo about the size of

Buteo jamaicensis and the holotype of Egretta subfluvia, an egret about the size of Egretta ibis. This locality probably represents a pond environment with some marine influence (Becker, 1985a).

Haile VB local fauna. The meager avifauna from this local fauna consists of several specimens of an indeterminate species of anatid. The paleoenvironment of this site was highly aquatic as shown by the abundant material of the crocodylian, Gavialosuchus.

Haile VI local fauna. Birds known from here include the holotype of Palaeostruthus eurius and several specimens of an indeterminate species of duck. Based on the birds, little can be said of the paleoecology of this locality.

Haile XIXA local fauna. Avian taxa from here include a cormorant and a few specimens of anatids. Further studies on the paleoecology of this site await additional systematic studies on the vertebrates present.

Bone Valley Mining District. While large numbers of fossil birds have been collected from here, it represents the most limited for paleoecological analysis because of collection techniques. This mining district, which is well over 100 square miles in extent and is being systematically strip-mined, resulting in the moving of hundreds of thousands of cubic yards of sediment. Many specimens of fossil birds were collected from spoil areas in conjunction with the commerical collection of the more numerous shark teeth and mammalian cranial fragments. Because of these collection techniques, usually it is not possible to quantify the relative abundance of fossil specimens of birds, the volume of sediments from which they originated, the sedimentary

horizon from which they came, or their association with other fossil vertebrates.

Like the Love Bone Bed, the Bone Valley avifauna is dominated by aquatic birds. However, in sharp contrast, the most abundant taxa present are marine. Birds from the Bone Valley Mining District included in this study are 3 species of grebe, 2 species of cormorant, an anhinga, 2 herons, 2 storks, an ibis, an osprey, 4 species of hawks or eagles, a goose, 4 species of duck, a turkey, a crane, a rail, a flamingo, 5 species of shorebird, and an owl. There is abundant material of Phalacrocorax wetmorei, Aythya sp., and Phoenicopterus floridanus. Other pelagic species, which were not included in this study, but are abundantly represented, include several (3?) species of alcids, loons, Larus elmorei, 2 species of Sula, and a species of Morus. Fossil material still occurs in about the same proportions as was reported by Brodkorb (1955a), even though the number of taxa in this avifauna have increased. By far the most common taxon in this deposit is the cormorant, Phalacrocorax wetmorei. The abundance of cormorants, sulids, and gulls argues for a near-shore marine environment.

Brodkorb (1955) suggested that the large concentrations of seabirds, especially cormorants, probably represented a breeding colony. For future consideration of this hypothesis, I note that there is a very low frequency of sub-adult specimens in the collections from Bone Valley. I have been unable to find comparable data on Recent breeding colonies.

It has also been suggested (Brodkorb, 1955; and references therein) that the large concentrations of fossil birds were responsible for the formation of the phosphorite deposits. Current hypotheses (Riggs, 1984) suggest that bacteria at the water-sediment interface are responsible for

the primary formation of phosphate grains from the upwelling of nutrient-rich waters. I suggest that the fossil birds in the Bone Valley Deposits are present as a result of the abundant food supplies in these nutrient-rich waters, rather than being the direct cause of it.

Manatee County Dam Site. The only avian taxon known from this local fauna is one specimen representing Phalacrocorax cf. P. wetmorei. Based on the available information pertaining to the geology, vertebrate fauna, and geographic location, this locality is in all aspects essentially an outlier of the Bone Valley local fauna discussed above. All comments pertaining to the paleoecology of Bone Valley also apply to this local fauna.

SR-64. Fossil birds from this locality include the cormorant Phalacrocorax wetmorei, loons, the flamingo, Phoenicopterus cf. P. floridanus, and alcids. As with the Manatee County Dam Site above, all available information about the geology, vertebrate fauna and geographic location indicates this locality is an outlier of the Bone Valley local fauna. See paleoecological comments under Bone Valley Mining District above.

CHAPTER VI
BIOCHRONOLOGY AND FAUNAL DYNAMICS

Introduction

The following analysis of the biochronology and faunal dynamics of the Neogene (23 mybp to 1.8 mybp) avifauna of North America takes much of its information from an accompanying project (Becker, ms.), which updates and reviews the Neogene records of the North American avifauna. This fossil record is still very incomplete in many areas, and its interpretation will doubtlessly change as new material becomes available and previously described material is restudied. I should also note that the current record of fossil birds suffers from decades of a typological systematic approach, with many species, and even genera, being based more on geography and on geologic age than on differences in morphology.

Faunal Dynamics

Remarks. Among the assumptions necessary to calculate faunal dynamic parameters are the following:

- (1) All taxa are correctly identified, are taxonomically valid, and are correctly placed systematically.
- (2) The stratigraphic context of the fossil specimens is known and the specimen is correctly placed in a local fauna.
- (3) The local fauna is correctly placed in geologic time.
- (4) Taxa are correctly divided into marine and non-marine groups.

In one or another instance, each of these assumptions is surely violated. Much work still remains to be done to verify some of the

supposed relationships of fossil birds suggested by previous authors and to correct erroneous locality information. However, the value of such investigations on fossil birds include:

- (1) Demonstration of general trends in avian faunal dynamics in the Neogene of North America. Major trends should still be evident, even though they are based on incomplete or partially correct data.
- (2) Taxa which do not parallel the general trend may be selected for further investigations.
- (3) Specific geographic areas and/or time intervals can be featured in future work.
- (4) Specific groups can be easily isolated, such as those of interest from a zoogeographical standpoint.

Formulae used to calculate the parameters appearing in these tables are presented and defined in the methods section, and abbreviations are given in Table 6.1. The separation of taxa into marine and non-marine groups is based on the habitats used by the majority of living congeners.

The Local Faunas

The Neogene localities that have produced avian specimens are not uniformly distributed in geologic time. Of 133 local faunas surveyed, 3.8% (5) are late Arikareean, 8.3 % (11) are Hemingfordian, 13.5 % (18) are Barstovian, 22.6 % (30) are Clarendonian, 30.1 % (40) are Hemphillian, and 21.8% (29) are Blancan in age. Or stated slightly differently, 74.4% (99/130) of the localities examined are from the last 41.0 % (Clarendonian to Blancan; 8.7 MA / 21.2 MA) of the Neogene. If only the published localities are used, instead of the total number of localities, the percentages are roughly comparable, but the absolute values are much lower (see Table 6.2).

An index of relative sampling may be calculated to adjust for the unequal lengths of time represented by these discrete NALMAs (North American Land Mammal Ages) and to take into account the number of sampling sites. The number of local faunas of a given NALMA are divided by the duration of that NALMA (Table 6.2). This shows that the last three NALMAs of the Neogene are better sampled than the first three by a factor of 2 or 3.

When the local faunas are further divided into marine and non-marine groups, even greater discrepancies in the representations of the NALMAs are apparent. In general the non-marine local faunas outnumber the marine local faunas by at least a factor of 3 to 1 (Table 6.2; 6.3; and Figure 6.4).

Additional comparisons can be made between the number of published versus unpublished localities. While these comparisons are biased by the collections I have been able to examine, marine avifaunas have been more completely described than terrestrial ones (compare Table 6.3; 6.4). The fossil avifaunas from nearly one-half of all terrestrial local faunas in which birds are present are entirely unstudied and unreported in the literature. As all major collections in the United States were not examined, this is certainly an underestimate of the amount of work left to be done and underscores the preliminary nature of this examination of faunal dynamics.

The Neogene Avifauna

The combined sample of all families and genera will be considered first, then reconsidered separately in marine and non-marine groups.

Families. The easiest statistic to calculate is the number of families present in a given NALMA. In the late Arikareean 8 familes are present of which 5 (63%) survive to the present. The number of families rapidly increase to 18 (17 surviving; 94%) in the Hemingfordian, 31 (30 surviving; 97%) in the Barstovian, 37 (36 surviving; 97%) in the Clarendonian, 40 (39 surviving; 98%) in the Hemphillian, and 41 (40 surviving; 98%) in the Blancaan. By the Barstovian a majority of the living families with a fossil record have appeared (Table 6.1).

Genera. The diversity (S_i) of the genera in the Neogene of North America begins with 10 (2 surviving; 20%) in the late Arikareean, 28 (11 surviving; 39%) in the Hemingfordian, 38 (22 surviving; 56%) in the Barstovian, 61 (43 surviving; 70%) in the Clarendonian, 78 (65 surviving; 83%) in Hemphillian, and increases to 98 (88 surviving; 90%) in the Blancaan.

Originations (O_i) and Extinctions (E_i) are given in Table 6.2. These parameters are the simple counts of the first and last appearance, respectively. Nine genera first appear in the late Arikareean. This increases to about 20 in both the Hemingfordian and Barstovian and then increases again to about 30 in the Clarendonian, Hemphillian, and Blancaan. Five extinctions occur in the late Arikareean, then 8 extinctions occur in each of the succesive NALMAs, with the exception of the Clarendonian, which records 12 extinctions.

The raw counts of origination and extinctions are adjusted for the unequal time interval in each of the NALMAs by dividing each count by the duration of the given NALMA to produce Origination rates (O_r) and Extinction rates (E_r) in Table 6.2.

Origination rates show a peak during the Hemingfordian, a very large increase in the Clarendonian, a decrease in the Hemphillian, although not to pre-Clarendonian level, then an additional increase in the Blancan. Extinction rates tend to be much lower than origination rates, but show a roughly parallel trend. Again, a high value is noted in the Clarendonian.

Turnover rates (T), or the numerical average of origination rates and extinction rates, predictably parallel the trends in origination and extinction rates described above. Running means (R_m), or the diversity minus the average of originations and extinctions of a given land mammal age, increase at a decreasing rate throughout the Neogene.

Turnover rates per genus (T/R_m) show a high value in the late Arikareean, decrease through the Barstovian, then peak in the Clarendonian, to decrease and show a low rate through to the end of the Neogene.

Marine versus Non-marine

A more instructive approach is to divide the North American avifauna into marine and non-marine subgroups and then compare and contrast these two broad divisions (Table 6.3; 6.4 and Figure 6.1; 6.2). The following observations result.

- (1) The North American marine avifauna is essentially established at a diversity of 20 to 25 genera by the Clarendonian. The North American non-marine avifauna is roughly stable at a diversity of 3 genera during the late Arikareean and Hemingfordian. From this NALMA through the remainder of the Neogene, diversity increases from 13 to 26 genera by the Blancan.

- (2) The absolute number of genera which become extinct is roughly stable over most of the Neogene with about 2 generic extinctions per million years in the marine avifauna and about 7 generic extinctions per million years in the non-marine avifauna.
- (3) In the marine avifauna, the rate of origination peaks during the Clarendonian with 4.4 new genera appearing per million years.
- (4) In the non-marine avifauna, there are peaks in the generic origination rates during the Hemingfordian, Clarendonian and Blancan Land Mammal Ages, with 6, 8, and 10 genera appearing per million years, respectively. These peaks rise above a background rate of 2 to 4 genera appearing per million years in the intervening NALMAs, or roughly a cyclic 2- to 4-fold change.
- (5) Extinction rates are typically low in the marine avifauna throughout the Neogene. With the exception of the Clarendonian, which shows an extinction rate of 2 genera per million years, all other NALMAs have an extinction rate much less than 1.0 extinction per million years. In the non-marine avifauna, extinction rates average from 1.0 to 2.8 generic extinctions per million years.
- (6) Turnover rates are consistently low in the Marine avifauna, with the highest turnover rate being in the Clarendonian. In non-marine avifauna, turnover peaks appear in alternating mammal ages (in the Hemingfordian, Clarendonian, and Blancan). These peaks in turnover represent a 2- to 3-fold increase over the rates in the intervening NALMAs. Fluctuations in the turnover rates are governed more by changes in origination rate than by changes in extinction rates.
- (7) The per-genus turnover rate (T/R_m) in marine avifauna is high in the late Arikareean (1.68) and then drops to approximately 0.20 through

the Clarendonian. In the Hemphillian and the Blancan it decreases again to less than 0.1. In the non-marine avifauna the turnover rate is 0.6 and 0.4 in the late Arikareean and Hemingfordian respectively, and a rate of 0.2 in the Clarendonian. Other mammal ages have a rate of 0.1 or less. The extremely high per-genus turnover rate in the Arikareean may be an artifact of the low sample size in this NALMA.

Discussion

Several factors could produce the results presented above, including real changes in fossil avifaunas, but also including invalid assumptions or errors in sampling. Certainly an obvious cause for some of the changes in faunal dynamics is the unequal distribution of localities within each mammal age. The absence of extinctions in the Hemingfordian and Barstovian is probably an artifact resulting from an impoverished prior record of taxa. The Clarendonian is the first NALMA in the Neogene with a large number of both marine and non-marine localities. This accounts at least for part of the peak in Or (marine) and the resultant peak in turnover.

The mammalian fossil record in the Neogene has long been known to consist of sequences of relatively long-lived "chronofaunas" whose boundaries do not coincide with the boundaries of the NALMAs. It is equally possible that birds exhibit a similar pattern of long periods of faunal stasis with relatively rapid periods of turnover at the ends of these periods. There is no a priori reason that these "avian" boundaries would correspond with the "mammalian" boundary of the NALMA, or even with the boundary of the mammalian chronofauna. Further work is needed to reconstruct the database of Neogene localities from one keyed into

relative time (NALMAs) to one keyed to absolute time. This database could then be clustered into "natural" groups of geological ranges of species to discriminate between the lack of localities and real turnover.

Vuilleumier (1984) examined the faunal turnover of the South American avifauna and has recently (in press) expanded his investigations to include the late Neogene North American fossil record of birds. It is difficult to make comparisons between his study and the results presented above because of the time scales used. The faunal parameters which Vuilleumier (1984, in press) presents, are based on a division of geologic time into Epochs, which have vastly uneven durations (Miocene, 17 MA; Pliocene, 2.5 MA). Many of the finer scale events presented above would not be apparent in Vuilleumier's parameters.

The faunal dynamics of mammals have been extensively investigated (Webb, 1976, Marshall, et al., 1982). Table 6.5 compares the most recent information on faunal dynamics of mammals (Marshall, et al., 1982) with those for birds. Generic extinction rates, generic origination rates, and turnover rates are substantially higher for mammals than for birds.

One possible explanation is that mammals are evolving at a much faster rate than are birds. However, considering the great diversity of the Recent avifauna and the comparable amount of morphological difference between equivalent taxonomic ranks of birds and mammals (Wyles et al., 1983), this explanation seems at best, only partial.

A more likely explanation is that the differences in faunal dynamic parameters between birds and mammals are due to the use of different types of taxonomic characters. In systematics of fossil avian species, the post-cranial skeleton is used almost exclusively. Conversely, in fossil mammals, dental morphology is usually used. As the post-cranial

skeleton is likely to be much more conservative as a systematic character than tooth morphology, a slower turnover rate in birds would not be unexpected.

Biochronology

The following preliminary list of taxa represents the first attempt at using fossil birds as biochronologically useful taxa. This list is based on the current record of avian genera from the Neogene of North America, with taxa of questionable validity being omitted. The following list will doubtlessly change and increase as our knowledge of avian evolution in the Neogene becomes more complete.

LATE ARIKAREAN. First Appearance: Morus.

Last Appearance: Plotopteridae.

HEMINGFORDIAN. First Appearance: Puffinus, Anhinga, Sula,
Dendrocygnini, Anatini, Palaeoborus, Neophrontops, Falco, Rallidae,
Megapaloelodus, Burhinus, Strigidae. Last Appearance: None identified.

BARSTOVIAN. First Appearance: Gavia, Podicipedidae, Diomedea,
Fulmarus, Phalacrocorax, Microsula, Osteodontornis, Ardea, Anserini,
Mergini, Vulturidae, Pandion, Rallus, Laridae, Stercorariidae, Alcinae,
Corvidae. Last Appearance: None identified.

CLARENDRONIAN. First Appearance: Rollandia, Tachybaptus, Oceanodroma,
Miosula, Plegadis, Egretta, Ardeola, Mycteria, Ciconia, Pliogyps, Fulica,
Grus, Limosa, Phoenicopterus, Jacana, Alca, Cephus, Cerorhinca, Uria,
Aethia, Praemancalla, Tytonidae. Last Appearance: Osteodontornis,
Microsula.

HEMPHILLIAN. First Appearance: Podiceps, Podilymbus, Pelecanus,
Eudocimus, Nycticorax, Cygnini, Bucephala, Oxyura, Haematopus, Calidris,
Larus, Pinguinus, Mancalla. Last Appearance: Pelagornithidae,
Balearicinae, Premancalla, Megapaloelodus.

BLANCAN. First Appearance: Aechmophorus, Botaurus, Colinus, Meleagris,
Ptychoramphus, Titanis, Sterna. Last Appearance: Miosula, Pliogyps,
Mancalla.

Table 6.1. Number of families and genera present in each North American Land Mammal Age and the percentage of those which are still living. See text for discussion of the division of families and genera into marine and non-marine groups. Abbreviations: L. ARIK. — late Arikareean (23.0 - 20.0 mybp), HEMING. — Hemingfordian (20.0 - 16.5 mybp), BARST. — Barstovian (16.5 - 11.5 mybp), CLAR. — Clarendonian (11.5 - 9.0 mybp), HEMP. — Hemphillian (9.0 - 4.5 mybp), BLAN. — Blancan (4.5 - 1.8 mybp). North American genera which lack a fossil record are omitted from this table.

	<u>L. ARIK.</u>	<u>HEMING.</u>	<u>BARST.</u>	<u>CLAR.</u>	<u>HEMP.</u>	<u>BLANC.</u>
Number families present						
Marine	3	3	9	10	12	11
Non-marine	5	15	22	27	28	30
Total	8	18	31	37	40	41
Number (%) living families						
Marine	1 (33)	2 (66)	8 (89)	9 (90)	11 (92)	11 (100)
Non-marine	4 (80)	15 (100)	22 (100)	27 (100)	28 (100)	29 (97)
Total	5 (63)	17 (94)	30 (97)	36 (97)	39 (98)	40 (98)
Number genera present						
Marine	3	3	12	21	26	26
Non-marine	7	25	26	40	52	72
Total	10	28	38	61	78	98
Number (%) living genera						
Marine	1 (33)	1 (100)	9 (75)	14 (67)	22 (85)	24 (92)
Non-marine	1 (14)	8 (32)	13 (50)	29 (73)	43 (83)	64 (89)
Total	2 (20)	11 (39)	22 (58)	43 (70)	65 (83)	88 (90)

Table 6.2 Faunal dynamics of the North American Neogene avifauna. Abbreviations as in Table 6.1.

	<u>L.</u>	<u>ARIK.</u>	<u>HEMING.</u>	<u>BARST.</u>	<u>CLAR.</u>	<u>HEMP.</u>	<u>BLANG.</u>
Duration (MA)	3	3.5	5	2.5	4.5	2.7	
Localities (Published)	5 (5)	11 (6)	18 (12)	30 (22)	40 (25)	29 (16)	
Sampling Index	1.67	1.71	2.40	8.80	5.56	5.93	
Number of genera (Si)	10	28	38	61	78	98	
Originations (No.)	9	23	18	31	29	29	
Extinctions (No.)	5	8	8	12	9	7	
Running mean (Rm)	3.00	12.50	25.00	39.50	59.00	80.00	
Origination Rate	3.00	6.57	3.60	12.40	6.44	10.74	
Extinction Rate	1.67	2.29	1.60	4.80	2.00	2.59	
Turnover Rate (T)	2.34	4.43	2.60	8.60	4.22	6.67	
T/Rm	0.78	0.35	0.10	0.22	0.07	0.08	
T/Si	0.23	0.16	0.07	0.14	0.05	0.07	

Table 6.3 Faunal dynamics of the marine Neogene birds from North America. Abbreviations as in Table 6.1.

	L.	ARIK.	HEMING.	BARST.	CLAR.	HEMP.	BLANC.
Duration (MA)	3	3.5	5	2.5	4.5	2.7	
Localities (Published)	3 (3)	1 (1)	3 (3)	8 (8)	11 (10)	1 (1)	
Sampling Index	1.00	0.29	0.60	3.20	2.22	0.37	
Number of genera (Si)	3	3	12	21	26	26	
Originations (No.)	3	2	9	11	10	2	
Extinctions (No.)	2	0	2	5	2	2	
Running mean (Rm)	0.50	2.00	6.50	13.00	20.00	24.00	
Origination Rate	1.00	0.86	1.80	4.40	2.22	0.74	
Extinction Rate	0.67	0.00	0.40	2.00	0.44	0.74	
Turnover Rate (T)	0.84	0.43	1.10	3.20	1.33	0.74	
T/Rm	1.68	0.21	0.17	0.25	0.07	0.03	
T/Si	0.28	0.14	0.09	0.15	0.05	0.03	

Table 6.4 Faunal dynamics of non-marine Neogene birds of North America. Abbreviations as in Table 6.1.

	<u>L.</u>	<u>ARIK.</u>	<u>HEMING.</u>	<u>BARST.</u>	<u>CLAR.</u>	<u>HEMP.</u>	<u>BLANC.</u>
Duration (MA)	3	3.5	5	2.5	4.5	2.7	
Localities (Published)	2 (2)	10 (5)	15 (9)	22 (14)	29 (15)	28 (15)	
Sampling Index	0.67	1.43	1.80	5.60	3.33	5.56	
Number of genera (Si)	7	25	26	40	52	72	
Originations (No.)	6	21	9	20	19	27	
Extinctions (No.)	3	8	6	7	7	5	
Running mean (Rm)	2.50	10.50	18.50	26.50	39.00	56.00	
Origination Rate	2.00	6.00	1.80	8.00	4.22	10.00	
Extinction Rate	1.00	2.29	1.20	2.80	1.56	1.85	
Turnover Rate (T)	1.50	4.15	1.50	5.40	2.89	5.93	
T/Rm	0.60	0.40	0.08	0.20	0.07	0.11	
T/Si	0.21	0.17	0.06	0.14	0.06	0.08	

Table 6.5. Comparisons of avian and mammalian faunal dynamics. Avian parameters include only non-marine faunas, from Table 6.4. Mammalian parameters are from Marshall et al. (1982). The mammalian parameters for the Hemphillian and Blancan are recalculated to account for the use of a different duration of these NALMAS.

	<u>AVIAN</u>		<u>MAMMALIAN</u>	
	<u>CLAR.</u>	<u>HEMP.</u>	<u>BLANC.</u>	<u>HEMP.</u>
Running mean (Rm)	26.50	39.00	56.00	52.00
Origination rate (or)	8.00	4.22	10.00	17.20
Extinction rate (Er)	2.80	1.56	1.85	14.80
Turnover rate (T)	5.40	2.89	5.93	16.00
Per-genus Turnover (T/Rm)	0.20	0.07	0.11	0.31
T/Si	0.14	0.06	0.08	0.17
				0.14
				0.18

Figure 6.1. Distribution of avian genera and localities through geologic time. Abbreviations as in Table 6.1.

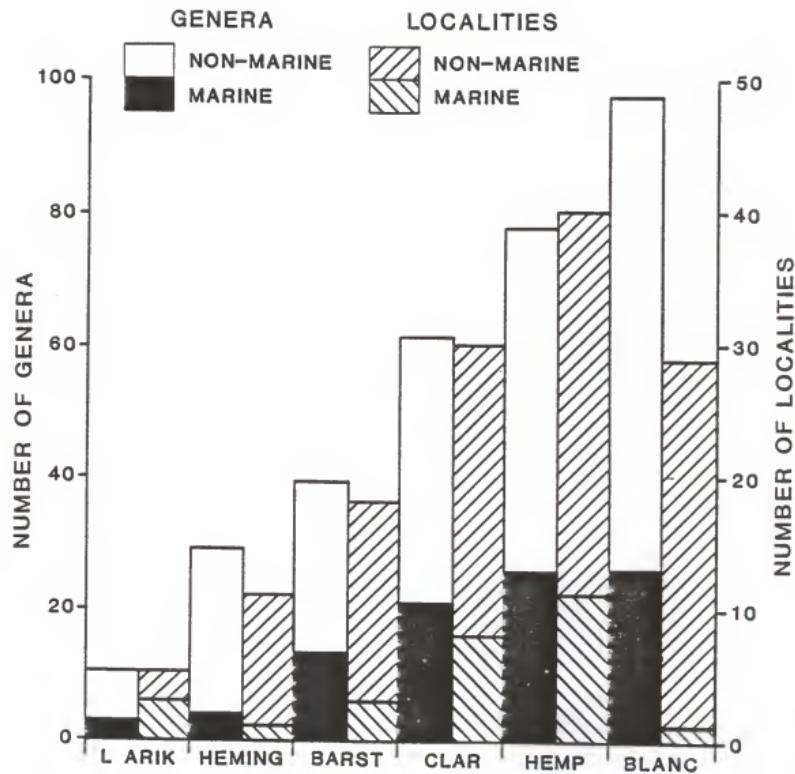
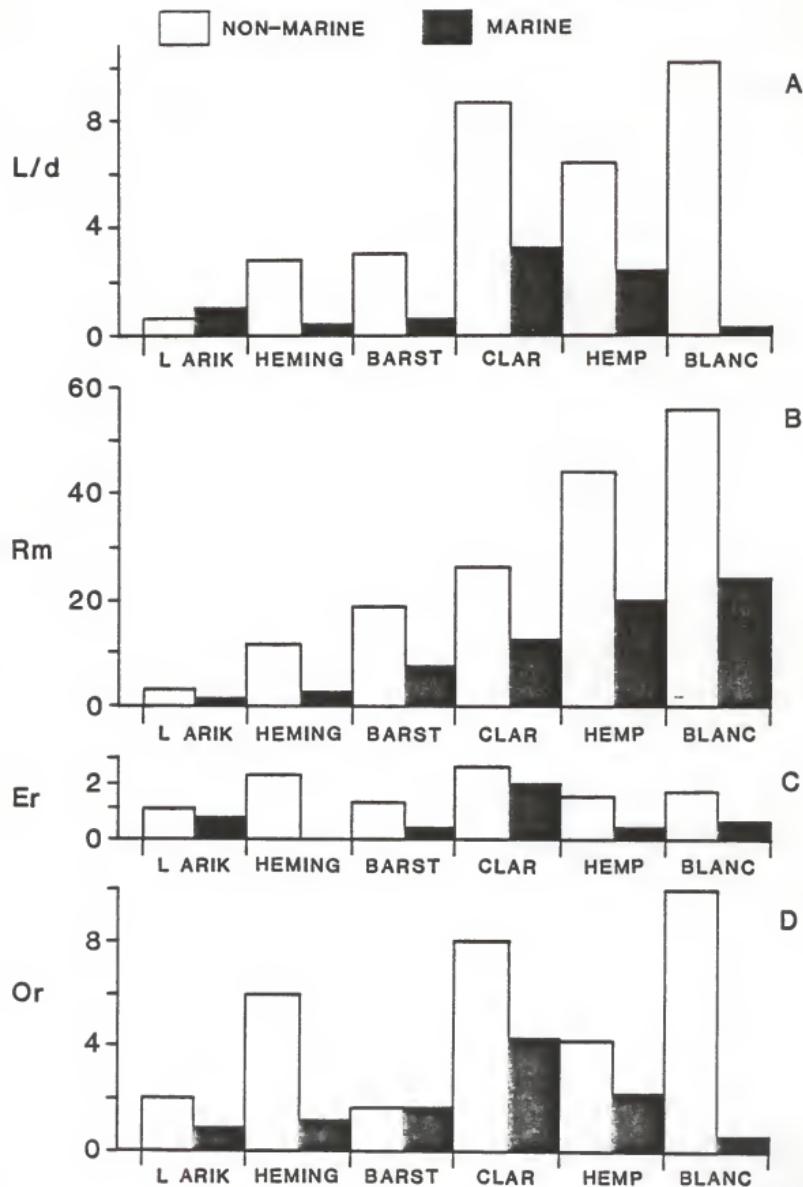


Figure 6.2. Graphic representation of avian faunal dynamic parameters. A. Number of localities per million years per NALMA. B. Running mean per NALMA. C. Extinction rate per NALMA. D. Origination rate per NALMA. Abbreviations as in Table 6.1.



CHAPTER VII SUMMARY

This study has examined three aspects of avian paleontology--systematics, paleoecology, and biochronology and faunal dynamics.

Systematics

It has first focused on the systematics of the non-marine fossil birds from the late Miocene and early Pliocene of Florida. 78 taxa have been identified in this study. Grebes (Family Podicipedidae) are represented by 6 taxa. A species of Tachybaptus is abundant in the Love Bone Bed local fauna and is also present from McGehee Farm. Rollandia is known from a few specimens from the Love Bone Bed, Mixson, and McGehee Farm. The skeleton of this species is slightly more robust than that of the living Rollandia rolland chilensis. A small species of Podilymbus is known from Mixson. The Bone Valley Mining District has produced specimens of 3 grebes--Podilymbus cf. P. podiceps, Podiceps sp. and Pliodytes lanquisti. All are rare members of the Bone Valley avifauna.

Pelecaniformes were represented by 2 or possibly 3 species of cormorants (Family Phalacrocoracidae) and 1 or possibly 2 species of anhinga (Family Anhingidae). The cormorant Phalacrocorax wetmorei is one of the best represented Neogene fossil species, with well over 500 specimens known. Almost every skeletal element is known. Phalacrocorax sp. A. is known from the Love Bone Bed, McGehee and probably Haile XIXA. The anhinga, Anhinga grandis, is known from the

Love Bone Bed and from McGehee Farm. It is larger than the living New World anhinga and is fairly completely known.

Six species of heron (family Ardeidae) are present. These include 2 species of Ardea, at least 2 species of Egretta, a species of Ardeola, and a single species of Nycticorax. Herons are rare members of fossil avifaunas.

Four storks are present as are 3 species of ibis. Storks (Family Ciconiidae) include a species of Mycteria from the Love Bone Bed and McGehee and 3 species of Ciconia, distributed between the Love Bone Bed, Mixson Bone Bed, and Bone Valley. This shows that storks were more diverse in the late Miocene and early Pliocene of North America than they are today. Ibises (Family Platialeidae) include a species of Eudocimus from the Bone Valley Mining District, and a specimen of Plegadis cf. P. pharangites and one representing a large species of indeterminate ibis from the Love Bone Bed.

Nine taxa of accipitriform birds are present, including a species of New World Vulture (Family Vulturidae), 1 or possibly 2 species of Osprey (Family Pandionidae), and 7 species of hawk or eagle (Family Accipitridae). Of note from the Love Bone Bed is an undescribed species of vulture, Pliogyps, and the most primitive species of osprey, Pandion lovensis, now known. An indeterminate species of Pandion, ?Haliaeetus sp., Aquila sp. A., and an indeterminate genus are all known from the Bone Valley Mining District. A species of Buteo near the size of Buteo jamaciensis occurs in the Withlacoochee River 4A local fauna.

Waterfowl (Family Anatidae) are common, with 5 species of geese and 8 species of ducks being present. Of note is a well-represented species of Dendrocygna from the Love Bone Bed which cannot be distinguished from

the living species of this genus. A very small species of teal, Anas sp. A., is also abundant in the Love Bone Bed local fauna. This species may represent the smallest species of the genus Anas now known. Other species of ducks and geese are common in these localities. A tadorine duck is known from one specimen from the Bone Valley Mining District.

Gallinaceous birds are poorly represented. Two species of turkeys (Family Phasianidae), each known from a single specimen, are known. One is referable to the genus Meleagris and the other is not referable to a genus.

Gruiform birds are also common with 4 species of crane (Family Gruidae) and 4 species of rail (Family Rallidae) being known. Of note is an undescribed species of primitive rail, which is known from abundant material from the Love Bone Bed and from a few specimens from the McGehee Farm local fauna. A specimen of a balearicine crane from the Bone Valley Mining District represents the last occurrence of this subfamily of cranes in North America. Today this subfamily is only known from Africa south of the Sahara. Cranes are also shown to be much more diverse in North America in the Miocene than in Pleistocene or Recent avifaunas.

Two species of flamingos (Family Phoenicopteridae; genus Phoenicopterus) are known. They are present in the Love Bone Bed local fauna, the McGehee Farm local fauna and from the Bone Valley. At least 2 different species of flamingo survived in North America until the Pleistocene.

A jacana, or lily-trotter (Family Jacanidae), Jacana farrandi, is known from the Love Bone Bed and from McGehee Farm. This distinctive genus is usually not found north of Mexico today.

A number of shorebirds (Family Scolopacidae) are known. Most are small and are tentatively referred to the genus Calidris.

Two owls are known. One is an undescribed genus (Family Tytonidae) which appears to be related to the barn owl and the grass owl of southeast Asia. Another (Family Strigidae), probably in the genus Bubo, is known from Bone Valley.

Three perching birds (Order Passeriformes) are present. All are poorly known.

The most diverse localities are the Love Bone Bed local fauna with approximately 44 taxa and the Bone Valley Mining District with approximately 41 taxa, 31 of which were studied in this paper. These localities are the most diverse non-marine and marine avifaunas, respectively, known in North America prior to the Pleistocene. Other localities are much less diverse. Approximately 14 taxa are represented at McGehee Farm, while the other localities included in this study typically have fewer than 3 or 4 taxa present.

Paleoecology

The second aspect of this study focused on paleoecology. Birds from two environments dominate the late Miocene and early Pliocene localities in Florida. Birds from the Bone Valley Mining District, SR-64, and Manatee County Dam are interpreted as being from near-shore marine environments. Abundantly represented taxa from other localities, such as the Love Bone Bed and McGehee Farm, are interpreted as representing freshwater ponds and streams, with marshes, mudflats, and estuaries not far removed. More terrestrial localities are either very poorly represented or lacking for this time period in Florida.

Biochronology and Faunal Dynamics

The final aspect of this dissertation focused on the biochronology and faunal dynamics of the Neogene North American fossil record of birds. From the examination of 133 Neogene localities which have produced fossil birds, I show that the fossil localities which have produced fossil birds are not uniformly distributed in time, with nearly 75% of the localities occurring in the last 41% of the Neogene. A majority of the living families of North American birds which have a fossil record appear by the Barstovian. Generic diversity increases throughout the Neogene. The marine avifauna is essentially established by the Clarendonian at a level of 20 - 25 genera, while the non-marine avifauna increases continually. Generic origination rates peak for marine birds in the Clarendonian, but extinction rates remain low throughout the Neogene. Generic origination rates for non-marine birds show a cyclic nature every alternate Land Mammal Age.

A preliminary list of biochronologically important genera of birds is presented. As our knowledge of the North American Neogene avifauna expands and becomes more complete, this list can be revised and updated.

LITERATURE CITED

- American Ornithologists' Union. 1983. Check-list of North American Birds, 6th. edition. 877 pp.
- Ammon, L. von 1911. Bayerische Braunkohlen und ihre Verwertung. Münich. 82 pp.
- Ammon, L. von 1918. Tertiäre Vogelreste von Regensburg und die jungmiozene Vogelwelt. Abhandl. Naturwiss. Vereines zu Regensburg, 12:1-70.
- Arredondo, O. 1976. The great predatory birds of the Pleistocene of Cuba. Smithsonian Contributions to Paleobiology, 27:169-187.
- Auffenberg, W. 1954. Additional specimens of Gavialosuchus americanus (Sellards) from a new locality in Florida. Quarterly Journal of the Florida Academy of Sciences, 17:185-209.
- Auffenberg, W. 1963. The fossil snakes of Florida. Tulane Studies in Zoology, 10:131-216.
- Ballmann, P. 1969a. Die Vögel aus der altburdigalen Spaltenfüllung von Wintershof (West) bei Eichstaett in Bayern. Zitteliana, 1:5-60. 2 taflen.
- Ballmann, P. 1969b. Les Oiseaux Miocénes de la Grive-Saint-Alban (Isére). Geobios, 2:157-204, 26 fig. pl. 13-15.
- Baskin, J. A. 1980. Evolutionary reversal in Mylagaulus (Mammalia, Rodentia) from the late Miocene of Florida. American Midland Naturalist, 104:155-162.
- Baskin, J. A. 1981. Barbourofelis (Nimravidae) and Nimravides (Felidae), with a description of two new species from the late Miocene of Florida. Journal of Mammalogy, 62:122-139.
- Baskin, J. A. 1982. Tertiary Procyoninae (Mammalia: Carnivora) of North America. Journal of Vertebrate Paleontology, 2:71-93.
- Baumel, J. J., A. S. King, A. M. Lucas, J. E. Breazile, and H. E. Evans. 1979. Nomina Anatomica Avium. Academic Press, London. 637 pp.
- Becker, J. J. 1984. Additions to the late Pleistocene avifauna of Bradenton, Manatee County, Florida. Florida Scientist, 47:201-203.

- Becker, J. J. 1985a. Fossil herons (Aves: Ardeidae) of the late Miocene and early Pliocene of Florida. *Journal of Vertebrate Paleontology*, 5:24-31.
- Becker, J. J. 1985b. *Pandion lovensis*, a new species of Osprey from the late Miocene of Florida. *Proceedings of the Biological Society of Washington*, 98:314-320.
- Becker, J. J. 1985c. A late Pleistocene (Wisconsinian) avifauna from West Palm Beach, Florida. *Bulletin of the British Ornithologists' Club*, 105:37-40.
- Becker, J. J. ms. Birds of the Pliocene (Blancan) Oreana local fauna, Owyhee County, Idaho.
- Becker, J. J. ms. Neogene Avian Localities of North America.
- Becker, J. J. ms. Fossil Anhingas (Aves, Pelecaniformes, Anhingidae) of North America.
- Berta, A. and H. Galiano. 1983. *Megantereon hesperus* from the late Hemphillian of Florida, with remarks on the phylogenetic relationships of machairodonts (Mammalia, Felidae, Machairodontinae). *Journal of Paleontology*, 57:892-899.
- Berta, A. and H. Galiano. 1984. A Miocene amphicyonid (Mammalia: Carnivora) from the Bone Valley Formation of Florida. *Journal of Vertebrate Paleontology*, 4:122-125.
- Berta, A. and G. S. Morgan. in press. A new sea otter (Carnivora: Mustelidae) from the late Miocene and early Pliocene (Hemphillian) of North America. *Journal of Paleontology*.
- Blake, E. R. 1977. Manual of Neotropical Birds. Spheniscidae (Penguins) to Laridae (Gulls and Allies). Vol. 1. University of Chicago Press, Chicago. 674 pp.
- Breyer, J. A. 1981. The Kimballian land-mammal age: mene, mene, tekeli, upharsin (Dan. 5:25). *Journal of Paleontology*, 55:1207-1216.
- Brodkorb, P. 1952. A new rail from the Pleistocene of Florida. *Wilson Bulletin*, 64:80-82.
- Brodkorb, P. 1953a. Pleistocene birds from Haile, Florida. *Wilson Bulletin*, 65:49-50.
- Brodkorb, P. 1953b. A Pliocene flamingo from Florida. *Natural History Miscellanea*, No. 124:1-4.
- Brodkorb, P. 1953c. A Pliocene gull from Florida. *Wilson Bulletin*, 65:94-98.
- Brodkorb, P. 1953d. Review of Pliocene loons. *Condor*, 55:211-214.

- Brodkorb, P. 1953e. A Pliocene grebe from Florida. Annals and Magazine of Natural History, Series 12:953-954.
- Brodkorb, P. 1954a. A chachalaca from the Miocene of Florida. Wilson Bulletin, 66:180-183.
- Brodkorb, P. 1954b. Another new rail from the Pleistocene of Florida. Condor, 56:103-104.
- Brodkorb, P. 1955a. The avifauna of the Bone Valley Formation. Florida Geological Survey, Report of Investigations, 14:1-57.
- Brodkorb, P. 1955b. Pleistocene birds from Eichelberger Cave, Florida. Auk, 1:136-137.
- Brodkorb, P. 1956a. Two new birds from the Miocene of Florida. Condor, 58:367-370.
- Brodkorb, P. 1956b. Pleistocene birds from Crystal Springs, Florida. Wilson Bulletin, 68:158.
- Brodkorb, P. 1957. New passerine birds from the Pleistocene of Reddick, Florida. Journal of Paleontology, 31:129-138.
- Brodkorb, P. 1959. The Pleistocene avifauna of Arredondo, Florida. Bulletin of the Florida State Museum, Biological Sciences, 4:269-291.
- Brodkorb, P. 1960. Great auk and common murre from a Florida midden. Auk, 77:342-343.
- Brodkorb, P. 1963a. Fossil birds from the Alachua clays of Florida. Florida Geological Survey, Special Publication No. 2, Paper No. 4:1-17.
- Brodkorb, P. 1963b. Miocene birds from the Hawthorne formation. Quarterly Journal Florida Academy Science, 26:159-167.
- Brodkorb, P. 1963c. Catalogue of Fossil Birds. Part 1. (Archaeopterygiformes through Ardeiformes). Bulletin Florida State Museum, Biological Science, 7:180-293.
- Brodkorb, P. 1963d. A giant flightless birds from the Pleistocene of Florida. Auk, 80:111-115.
- Brodkorb, P. 1963e. An extinct grebe from the Pleistocene of Florida. Quarterly Journal of the Florida Academy of Sciences, 26:53-55.
- Brodkorb, P. 1964. Catalogue of Fossil Birds. Part 2. (Anseriformes through Galliformes). Bulletin Florida State Museum, Biological Sciences, 8:195-335.

- Brodkorb, P. 1967. Catalogue of Fossil Birds. Part 3. (Ralliformes, Ichtyornithiformes, Charadriiformes). Bulletin Florida State Museum, Biological Sciences, 11:99-220.
- Brodkorb, P. 1970. (Abstract). New discoveries of Pliocene birds in Florida. p. 74. In E. J. Brill (ed). Proceedings of the XVth International Ornithological Congress, Leiden.
- Brodkorb, P. 1971a. Catalogue of Fossil Birds. Part 4. (Columbiformes through Piciformes). Bulletin Florida State Museum, Biological Sciences, 15:163-266.
- Brodkorb, P. 1971b. Origin and Evolution of Birds. pp. 19-55. In. Avian Biology, Volume 1. Academic Press, New York and London.
- Brodkorb, P. 1978. Catalogue of Fossil Birds. Part 5. (Passeriformes). Bulletin Florida State Museum, Biological Sciences, 23:139-228.
- Brodkorb, P. 1980. A new fossil heron (Aves: Ardeidae) from the Omo Basin of Ethiopia, with remarks on the position of some other species assigned to the Ardeidae. Contributions in Science, Natural History Museum of Los Angeles County, 330:87-92.
- Brodkorb, P. and C. Mourer-Chauvire. 1982. Fossil anhingas (Aves: Anhingidae) from Early Man sites of Hadar and Omo, Ethiopia, and Olduvai Gorge, Tanzania. Geobios, 15:505-515.
- Brodkorb, P. and C. Mourer-Chauvire. 1984. A new species of cormorant (Aves: Phalacrocoracidae) from the Pleistocene of Olduvai Gorge, Tanzania. Geobios, 17:331-337.
- Brown, L. H. and D. Amadon. 1969. Eagles, Hawks, and Falcons of the World. Country Life, London.
- Campbell, K. E., Jr. 1976. An early Pleistocene avifauna from Haile XVA, Florida. Wilson Bulletin, 88:345-347.
- Campbell, K. E., Jr. 1979. The non-passerine Pleistocene avifauna of the Talara Tar Seeps, northwestern Peru. Publications in Life Sciences, Royal Ontario Museum, 118:1-203.
- Campbell, K. E., Jr. 1980. A review of the Rancholabrean avifauna of the Itchtucknee River, Florida. Contributions in Science, Natural History Museum of Los Angeles County, 330:119-129.
- Campbell, K. E., Jr. and E. P. Tonni. 1983. Size and locomotion in teratorns (Aves: Teratornithidae). Auk, 100:390-403.
- Carr, G. S. 1981. An early Pleistocene avifauna from Inglis, Florida. Ph. D. Dissertation. University of Florida, Gainesville.

- Cheneval, J. 1984. Les Oiseaux (Gaviiformes a Anseriformes) du Gisement Aquitanian de Saint-Gérand-le-Puy (Allier, France): Revision Systematique. *Paleovertebrata*, 14(2):33-115, 6 fig.
- Cracraft, J. 1971a. The humerus of the early Miocene cracid, Boreortalis laesslei Brodkorb. *Wilson Bulletin*, 83:200-201.
- Cracraft, J. 1971b. Systematics and evolution of the Gruiformes (Class Aves). 2. Additional comments of the Bathornithidae, with descriptions of new species. *American Museum Novitates*, 2449:1-14.
- Cracraft, J. 1973. Systematics and evolution of the Gruiformes (Class Aves). 3. Phylogeny of the suborder Grues. *Bulletin of the American Museum of Natural History*, 51:1-127.
- Cracraft, J. 1981. Toward a phylogenetic classification of Recent birds of the world (Class Aves). *Auk*, 98:681-714.
- Cracraft, J. 1982. Phylogenetic relationships and morphology of loons, grebes, and Hesperornithiform birds, with comments on the early history of birds. *Systematic Zoology*, 31:35-56.
- Cracraft, J. and P. V. Rich. 1972. The systematics and evolution of the Cathartidae in the Old World Tertiary. *Condor*, 74:272-283.
- Dall, W. H. and G. D. Harris. 1892. Correlation papers, Neogene. U. S. Geological Survey. *Bulletin* 84, 349 pp.
- Dixon, W. J. 1981. BMDP Statistical Software. University of California Press, Berkeley. 725 pp.
- Emslie, S. D. 1985. A new species of teal from the Pleistocene (Rancholabrean) of Wyoming. *Auk*, 102:201-205.
- Feduccia, A. 1968. The Pliocene rails of North America. *Auk*, 85:441-453.
- Feduccia, A. 1970. A new shorebird from the Upper Pliocene. *Journal of the Graduate Research Center, Southern Methodist University*, 38(3 and 4):58-60.
- Feduccia, A. 1975. Aves osteology. pp. 1790-1801. In R. Getty (ed.) *Sisson and Grossman's The Anatomy of the Domestic Animals*. W. B. Saunders, Philadelphia.
- Feduccia, A. and S. L. Olson. 1982. Morphological similarities between the Menurae and the Rhinocryptidae, relict passerine birds of the Southern Hemisphere. *Smithsonian Contribution to Zoology*, 366. 22 pp.
- Fisher, H. I. 1945. Locomotion in the fossil vulture *Teratornis*. *American Midland Naturalist*, 33:725-742.

- Ford, N. L. 1967. A Systematic Study of the Owls based on Comparative Osteology. Ph. D. Dissertation. University of Michigan, Ann Arbor.
- Friedmann, H. 1947. Geographic variations of the Black-bellied, Fulvous, and White-faced Tree Ducks. *Condor*, 49:189-195.
- Fürbringer, M. 1888. Untersuchungen zur Morphologie und Systematik der Vögel, zugleich ein Beitrag zur Anatomie der Stütz und Bewegungsorgane. 2 vol. Van Holkema, Amsterdam. 1751 pp. 30 pls.
- Gadow, H. 1893. Vögel. II. Systematischer Theil. In Dr. H. G. Bronn's Klassen und Ordnungen der Thier-Reichs, Vol. 6(4). C. F. Winter, Leipzig. 303 pp.
- Gilbert, B. M., L. D. Martin, and H. G. Savage. 1981. Avian Osteology. Author, Laramie, Wyoming. 252 pp.
- Hamon, J. H. 1959. Northern birds from a Florida Indian Midden. *Auk* 76:533-534
- Hamon, J. H. 1964. Osteology and paleontology of the passerine birds of the Reddick, Florida, Pleistocene. Florida Geological Survey, Geology Bulletin, 44:1-210.
- Harrison, C. J. O. 1981. A re-assignment of Amphipelargus [sic] majori from Ciconiidae (Ciconiiformes) to Ergilornithidae (Gruiformes). *Tertiary Research*, 3:111-112.
- Harrison, J. A. 1981. A review of the extinct wolverine, Pleisogulo (Carnivora: Mustelidae), from North America. *Smithsonian Contributions to Paleobiology*, 46:1-27.
- Harrison, J. A. and E. M. Manning. 1983. Extreme carpal variability in Teleoceras (Rhinocerotidae, Mammalia). *Journal of Vertebrate Paleontology*, 3:58-64.
- Hay, O. P. 1902. On the finding of the bones of the Great Auk (Plactus impennis) in Florida. *Auk*, 19:255-258.
- Hay, O. P. 1923. The Pleistocene of North America and its vertebrate animals from the states east of the Mississippi River and from the Canadian provinces east of longitude 95 degrees. Carnegie Institution of Washington, Publication, 322:i-viii,1-499.
- Hirschfeld, S. E. 1968. Vertebrate fauna of Nichol's Hammock, a natural trap. *Quarterly Journal of the Florida Academy of Sciences*, 31:177-189.
- Hirschfeld, S. E. and S. D. Webb. 1968. Plio-Pleistocene megalonychid sloths of North America. *Bulletin of the Florida State Museum, Biological Sciences*, 5:213-296.

- Holman, J. A. 1959. Birds and mammals from the Pleistocene of Williston, Florida. Bulletin of the Florida State Museum, Biological Sciences, 5:1-25
- Holman, J. A. 1961. Osteology of living and fossil New World Quails (Aves, Galliformes). Bulletin of the Florida State Museum, Biological Sciences, 6:131-233.
- Howard, H. 1929. The avifauna of Emeryville shellmound. University California Publication in Zoology, 32:301-394. 4 pls., 55 text figs.
- Howard, H. 1932a. A new species of Cormorant from Pliocene deposits near Santa Barbara California. Condor, 34:118-120.
- Howard, H. 1932b. Eagles and eagle-like vultures of the Pleistocene of Rancho La Brea, California. Carnegie Institution of Washington, Publication 429:1-82, 29 pls.
- Howard, H. 1942. A review of the American fossil storks. Carnegie Institution of Washington, Publication, 530:187-203, 1 pl.
- Howard, H. 1946. A review of the Pleistocene birds of Fossil Lake, Oregon. Carnegie Institution of Washington, Publication, 551:141-195.
- Howard, H. 1949. New avian records for the Pliocene of California. Carnegie Institution of Washington, Publication, 584:177-199.
- Howard, H. 1957. A new species of passerine bird from the Miocene of California. Contributions in Science, Natural History Museum of Los Angeles County, 9:1-16.
- Howard, H. 1964. Fossil Anseriformes. pp. 233-326. In J. Delacour (ed). Waterfowl of the World. Vol. 4. Country Life Ltd., London.
- Howard, H. 1965. A new species of cormorant from the Pliocene of Mexico. Bulletin Southern California Academy Science, 64:50-55.
- Howard, H. 1973. Fossil Anseriformes. General Corrections and Additions. pp. 371-378. In J. Delacour (ed). Waterfowl of the World. Second Edition. Vol. 4. Hamlyn Publishing Group Ltd., London.
- Howard, H. 1980. Illustrations of avian osteology taken from 'The Avifauna of Emeryville Shellmound'. Contributions in Science, Natural History Museum of Los Angeles County, 330:xxvii-xxxviii.
- Hulbert, R. C. 1982. Population dynamics of the three-toed horse Neohippurion from the late Miocene of Florida. Paleobiology, 8:159-167.
- Hull, D. L. 1970. Comtempory systematic philosophies. Annual Review of Ecology and Systematics. 1:19-54.

- Holman, J. A. 1959. Birds and mammals from the Pleistocene of Williston, Florida. Bulletin of the Florida State Museum, Biological Sciences, 5:1-25
- Holman, J. A. 1961. Osteology of living and fossil New World Quails (Aves, Galliformes). Bulletin of the Florida State Museum, Biological Sciences, 6:131-233.
- Howard, H. 1929. The avifauna of Emeryville shellmound. University California Publication in Zoology, 32:301-394. 4 pls., 55 text figs.
- Howard, H. 1932a. A new species of Cormorant from Pliocene deposits near Santa Barbara California. Condor, 34:118-120.
- Howard, H. 1932b. Eagles and eagle-like vultures of the Pleistocene of Rancho La Brea, California. Carnegie Institution of Washington, Publication 429:1-82, 29 pls.
- Howard, H. 1942. A review of the American fossil storks. Carnegie Institution of Washington, Publication, 530:187-203, 1 pl.
- Howard, H. 1946. A review of the Pleistocene birds of Fossil Lake, Oregon. Carnegie Institution of Washington, Publication, 551:141-195.
- Howard, H. 1949. New avian records for the Pliocene of California. Carnegie Institution of Washington, Publication, 584:177-199.
- Howard, H. 1957. A new species of passerine bird from the Miocene of California. Contributions in Science, Natural History Museum of Los Angeles County, 9:1-16.
- Howard, H. 1964. Fossil Anseriformes. pp. 233-326. In J. Delacour (ed). Waterfowl of the World. Vol. 4. Country Life Ltd., London.
- Howard, H. 1965. A new species of cormorant from the Pliocene of Mexico. Bulletin Southern California Academy Science, 64:50-55.
- Howard, H. 1973. Fossil Anseriformes. General Corrections and Additions. pp. 371-378. In J. Delacour (ed). Waterfowl of the World. Second Edition. Vol. 4. Hamlyn Publishing Group Ltd., London.
- Howard, H. 1980. Illustrations of avian osteology taken from 'The Avifauna of Emeryville Shellmound'. Contributions in Science, Natural History Museum of Los Angeles County, 330:xxvii-xxxviii.
- Hulbert, R. C. 1982. Population dynamics of the three-toed horse Neohippidion from the late Miocene of Florida. Paleobiology, 8:159-167.
- Hull, D. L. 1970. Comtempory systematic philosophies. Annual Review of Ecology and Systematics. 1:19-54.

- Jackson, D. A. 1976. The status of the Pliocene turtle Pseudomys caelata Hay and Chrysemys carri Rose and Weaver. *Copeia*, v-1976:655-659.
- Jackson, D. A. 1978. Evolution and fossil record of the chicken turtle, Deirochelys, with a re-evaluation of the genus. *Tulane Studies Zoology*, Botany, 20:35-55.
- Johnsgard, P. A. 1981. The Plovers, Sandpipers, and Snipes of the World. University of Nebraska Press, Lincoln. 493 pp.
- Johnsgard, P. A. 1983. Cranes of the World. Indiana University Press, Bloomington. xiii + 257 pp.
- Johnson, L. A. S. 1970. Rainbow's end: the quest for an optimal taxonomy. *Systematic Zoology*, 19:203-239.
- Jollie, M. J. 1976-1977. A contribution to the morphology and phylogeny of the Falconiformes. Parts 1-4. *Evolutionary Theory*, 1:285-298; 2:115-300; 3:1-142.
- Kahl, M. P. 1971. Social behavior and taxonomic relationships of the storks. *Living Bird*, 10:151-170.
- Kahl, M. P. 1972. A revision of the family Ciconiidae (Aves). *Journal Zoological*, London. 167:451-461.
- Kurochkin, E. N. 1980. Middle Pliocene rails from western Mongolia. Contribution in Science, Natural History Museum of Los Angeles County, 330:69-73.
- Leidy, J. and F. Lucas. 1896. Fossil vertebrates from the Alachua Clays. *Wagner Free Institute Science, Transactions*, 4:1-61.
- Ligon, J. D. 1965. A Pleistocene avifauna from Haile, Florida. *Bulletin of the Florida State Museum, Biological Sciences*, 10:127-158.
- Ligon, J. D. 1967. Relationships of the cathartid vultures. *Occasional Papers of the Museum of Zoology*, University of Michigan, 651:1-26.
- MacFadden, B. J. 1982. New species of primitive three-toed browsing horse from the Miocene Phosphate Mining District of Central Florida. *Florida Scientist*, 45:117-125.
- MacFadden, B. J. 1984. Astrohippus and Dinohippus from the Yephmerra local fauna (Hemphillian, Mexico) and implications for the phylogeny of one-toed horses. *Journal of Vertebrate Paleontology*, 4:273-283.
- MacFadden, B. J. and H. Galiano. 1981. Late Hemphillian cat (Mammalia: Felidae) from Bone Valley Formation of Central Florida. *Journal of Paleontology*, 55:218-226.

- MacFadden, B. J. and J. S. Waldrop. 1980. Nannipus phlegon (Mammalia, Equidae) from the Pliocene (Blancan) of Florida. Bulletin of the Florida State Museum, Biological Sciences, 25:1-37.
- MacFadden, B. J. and S. D. Webb. 1982. The succession of Miocene (Arikareean through Hemphillian) terrestrial mammalian localities and faunas in Florida. pp. 186-199. In: Scott, T. M. and S. B. Upchurch. Miocene of the southeastern United States. Tallahassee, Florida Department of Natural Resources, Bureau of Geology, Special Publication 25, 319 pp.
- Marshall, L. G., R. F. Butler, R. E. Drake, C. H. Curtis, and R. H. Tedford. 1979. Calibration of the Great American Interchange. Science, 204:272-279.
- Marshall, L. G., S. D. Webb, J. J. Sepkoski, Jr., and D. M. Raup. 1982. Mammalian evolution and the Great American Interchange. Science, 215:1351-1357.
- Martin, L. and R. M. Mengel. 1975. A new species of anhinga (Anhingidae) from the Upper Pliocene of Nebraska. Auk, 92:137-140.
- Martin, L. and R. M. Mengel. 1980. A new goose from the Late Pliocene of Nebraska with notes of variability and proportions in some Recent geese. Contributions in Science, Natural History Museum of Los Angeles County, 330:75-85.
- Mayr, E. 1969. Principles of Systematic Zoology. McGraw-Hill, New York. 428 pp.
- Mayr, E. 1981. Biological classification: toward a synthesis of opposing methodologies. Science, 214:510-516.
- Mayr, E. and G. W. Cottrell. 1979. Check-list of Birds of the World. Volume 1. 2nd Edition. Harvard University Press, Cambridge, Massachusetts.
- Mayr, E. and L. L. Short. 1970. Species taxa of North American birds. A contribution to comparative systematics. Publication of the Nuttall Ornithological Club, 9:1-127.
- McCoy, J. J. 1963. The fossil avifauna of Itchtucknee River, Florida. Auk, 80:335-351.
- Miller, A. H. 1944. An avifauna from the lower Miocene of South Dakota. University California Publication, Bulletin Department of Geological Sciences, 27:85-100.
- Miller, A. H. 1966. An evaluation of the fossil Anhingas of Australia. Condor, 68:315-320.
- Miller, L. 1925. Avian remains from the Miocene of Lompoc. Carnegie Institution of Washington, Publication, 349:107-117.

- Miller, L. 1929. A new cormorant from the Miocene of California. *Condor*, 31:167-172.
- Mourer-Chauvire, C. 1982. Les Oiseaux fossiles des Phosphorites du Quercy (Eocène supérieur à Oligocène supérieur): implications paléobiogeographiques. *Geobios, Mémoire Spécial* 6:413-426.
- Murray, B. G., Jr. 1967. Grebes from the late Pliocene of North America. *Condor*, 69:277-288.
- Murray, B. G., Jr. 1970. A redescription of two Pliocene cormorants. *Condor*, 72:293-298.
- Neill, W. T., H. J. Gut, and P. Brodkorb. 1956. Animal remains from four preceramic sites in Florida. *American Antiquity*, 21:383-395.
- Ober, L. D. 1978. The Monkey Jungle, a late Pleistocene fossil site in southern Florida. *Plaster Jacket*, 28:1-13.
- Olson, S. L. 1973. A classification of the Rallidae. *Wilson Bulletin*, 85:381-416.
- Olson, S. L. 1974a. A reappraisal of the fossil heron *Palaeophoxys columbiana* McCoy. *Auk*, 91:179-180.
- Olson, S. L. 1974b. The Pleistocene Rails of North America. *Condor*, 76:169-175.
- Olson, S. L. 1975a. An evaluation of the supposed Anhinga of Mauritius. *Auk*, 92:374-376
- Olson, S. L. 1976. A Jacana from the Pliocene of Florida (Aves: Jacanidae). *Proceedings of the Biological Society Washington*, 89:259-264.
- Olson, S. L. 1977a. The identity of the fossil ducks described from Australia by C. W. DeVis. *Emu*, 77:127-131.
- Olson, S. L. 1977b. A Synopsis of the Fossil Rallidae. pp. 339-373, figures 1-26. In S. D. Ripley. *Rails of the World: A Monograph of the Family Rallidae*. David R. Godine, Boston. 406 pp.
- Olson, S. L. 1978. The nomenclatural status of the taxa of fossil birds attributed to Auguste Aymard. *Proceedings of the Biological Society of Washington*, 91:444-449.
- Olson, S. L. 1981a. The museum tradition in ornithology---A response to Ricklefs. *Auk*, 98:193-195.
- Olson, S. L. 1981b. The generic allocation of *Ibis pagana* Milne-Edwards, with a review of fossil Ibises (Aves: Threskiornithidae). *Journal of Vertebrate Paleontology*, 1:165-170.

- Olson, S. L. in press. The Fossil Record of Birds. Avian Biology. Vol. 8. Academic Press, New York.
- Olson, S. L. and J. Farrand, Jr. 1974. Rhegminornis restudied: a tiny Miocene turkey. Wilson Bulletin, 86:114-120.
- Olson, S. L. and A. Feduccia. 1979. A Old World occurrence of the Eocene avian family Primobucconidae. Proceedings of the Biological Society of Washington, 92:494-497.
- Olson, S. L. and A. Feduccia. 1980. Relationships and Evolution of Flamingos (Aves: Phoenicopteridae). Smithsonian Contributions to Zoology, 316 73 pp.
- Olson S. L. and D. W. Steadman. 1981. The relationships of the Pedionomidae (Aves: Charadriiformes). Smithsonian Contributions to Zoology, 337. 25 pp.
- Ono, K. 1980. Comparative osteology of three species of Japanese cormorants of the Genus Phalacrocorax (Aves, Pelecaniformes). Bulletin National Science Museum, Ser. C (Geology), 6:129-151.
- Opdyke, N. D., D. R. Spangler, D. L. Smith, D. S. Jones, and R. C. Lindquist. 1984. Origin of the epeirogenic uplift of Pliocene-Pleistocene beach ridges in Florida and the development of the Florida karst. Geology, 12:226-228.
- Palmer, R. 1962. Handbook of North American Birds. Volume 1. Loons through Flamingos. Yale University Press, New Haven. 567 pp.
- Palmer, R. 1975. Handbook of North American Birds. Volume 3. Waterfowl (concluded). Yale University Press, New Haven. 560 pp.
- Palmer, R. 1976. Handbook of North American Birds. Volume 2. Waterfowl (first part). Yale University Press, New Haven. 521 pp.
- Patton, T. H. and B. E. Taylor. 1973. The Protoceratiniae (Mammalia, Tylopoda, Protoceratidae) and the systematics of the Protoceratidae. Bulletin of the American Museum of Natural History, 150:347-414.
- Payne, R. and C. Risley. 1976. Systematics and evolutionary relationships among the herons (Ardeidae). Miscellaneous Publications, Museum of Zoology, University of Michigan, 150:1-115.
- Peters, J. L. 1931. Check-list of Birds of the World. Volume 1. Harvard University Press, Cambridge, Massachusetts. 345 pp.
- Peters, J. L. 1934. Check-list of Birds of the World. Volume II. Harvard University Press, Cambridge, Massachusetts. 409 pp.
- Peters, J. L. 1940. Check-list of Birds of the World. Volume IV. Harvard University Press, Cambridge, Massachusetts. 291 pp.

- Peters, J. L. 1951. Check-list of Birds of the World. Volume VII. Harvard University Press, Cambridge, Massachusetts. 318 pp.
- Prange, H. D., J. F. Anderson, and H. Rahn. 1979. Scaling of skeletal mass to body mass in birds and mammals. *American Naturalist*, 113:103-122.
- Ray, C. E. 1957. A list, bibliography, and index of the fossil vertebrates of Florida. Florida Geological Survey Special Publication No. 3. 175 pp.
- Rea, A. M. 1983. Cathartid affinities: a brief overview. pp. 26-53. In S. R. Wilbur and J. A. Jackson (eds.). *Vultur Biology and Management*. University of California Press, Berkeley.
- Recher, H. F. and J. A. Recher. 1980. Why are there different kinds of herons? *Transactions of the Linnaean Society of New York*, 9:135-158.
- Rich, P. V. 1972. A fossil avifauna from the Upper Miocene Beglia Formation of Tunisia. *Notes Serv. Geol. Tunisie* 35. *Trav. Geol. Tunisienne* No. 5. Formation Beglia-Fasc. 1. p. 29-66. [not seen].
- Rich, P. V. 1976. The history of birds on the island continent Australia. *Proceedings 16th International Ornithological Congress*, Canberra, Australia. pp. 53-65.
- Rich, P. V. 1980. 'New World Vultures' with Old World affinities? *Contributions to Vertebrate Evolution*, 5:viii + 116.
- Rich, P. V. and C. A. Walker. 1983. A new genus of Miocene flamingo from East Africa. *Ostrich*, 54:95-104.
- Riggs, S. R. 1984. Paleoceanographic model of the Neogene phosphorite deposition, U. S. Atlantic continental margin. *Science*, 223:123-131.
- Ripley, S. D. 1977. Rails of the World. A Monograph of the Family Rallidae. Godine, Boston, Massachusetts. 406 pp.
- Ritchie, T. 1980. Two mid-Pleistocene avifaunas from Coleman, Florida. *Bulletin of the Florida State Museum, Biological Sciences*, 26:1-36.
- Schultz, C., M. Schultz, and L. Martin. 1970. A new tribe of saber-toothed cats (Barbourofelini) from the Pliocene of North America. *Bulletin University of the Nebraska State Museum*, 9:1-31.
- Sellards, E. H. 1916. Fossil vertebrates from Florida: A new Miocene fauna; new Pliocene species; the Pleistocene fauna. *Florida Geological Survey 8th Annual Report*, Tallahassee. pp. 77-102, pls. 10-14.
- Shipman, P. 1981. Life history of a fossil. Harvard University Press, Cambridge, Massachusetts. 222 pp.

- Shufeldt, R. W. 1917a. Report on fossil birds from Vero, Florida. In Sellards, E. H. On the association of human remains and extinct vertebrates at Vero, Florida. Journal of Geology, 25:18-19.
- Shufeldt, R. W. 1917b. Fossil birds found at Vero, Florida. Florida Geological Survey 9th Annual Report, Tallahassee. pp. 35-42.
- Shufeldt, R. W. 1918. Notes on some bird fossils from Florida. Auk, 35:357-358.
- Simpson, G. 1930. Tertiary land mammals of Florida. Bulletin American Museum of Natural History, 59:149-211.
- Simpson, G. G., A. Roe, and R. C. Lewontin. 1960. Quantitative Zoology. Harcourt, Brace, and Co., Inc. New York.
- Steadman, D. W. 1976. An addition to two Florida Pleistocene avifaunas. Auk, 93:645-646.
- Steadman, D. W. 1980. A review of the osteology and paleontology of Turkeys (Aves: Meleagridinae). Contributions in Science, Natural History Museum of Los Angeles County, 330:131-207.
- Steadman, D. W. 1981. A re-examination of Palaeostruthus hatcheri (Shufeldt), a late Miocene sparrow from Kansas. Journal of Vertebrate Paleontology, 1:171-173.
- Steadman, D. W. 1984. A middle Pleistocene (Late Irvingtonian) avifauna from Payne Creek, central Florida. Carnegie Museum of Natural History, Special Publication, 8:47-52.
- Steadman, D. W. and M. C. McKittrick. 1982. A Pliocene bunting from Chihuahua, Mexico. Condor, 84:240-241.
- Storer, R. W. 1963. Courtship and mating behavior and the phylogeny of the grebes. Proceedings of the XIII International Ornithological Congress, Ithaca. pp. 562-569.
- Storer, R. W. 1967. Observations on Rolland's Grebe. El Hornero, 10:339-350.
- Storer, R. W. 1976a. The behavior and relationships of the Least Grebe. Transactions of the San Diego Society of Natural History, 18:113-126.
- Storer, R. W. 1976b. The Pleistocene Pied-billed Grebes (Aves: Podicipedidae). Smithsonian Contribution to Paleobiology, 27:147-153.
- Strauch, J. G., Jr. 1978. The Cladistic Relationships of the Charadriiformes. Ph.D. dissertation. University of Michigan.

- Tedford, R. 1970. Principles and practices of mammalian geochronology in North America. Proceedings North American Paleontological Convention, Part F:666-703.
- Tedford, R. H., T. Galusha, M. F. Skinner, B. E. Taylor, R. W. Fields, J. R. Macdonald, J. Rensberger, S. D. Webb, and D. P. Whistler. in press. Faunal succession and biochronology of the Arikareean through Hemphillian interval (late Oligocene through late Miocene Epochs), North America. University of California Press, Berkeley.
- Terres, J. K. 1980. The Audubon Society Encyclopedia of North American Birds. Alfred A. Knopf, Inc., New York. 1110 pp.
- Tonni, E. P. 1980. The present state of knowledge of the Cenozoic birds of Argentina. Contributions in Science, Natural History Museum of Los Angeles County, 330:105-114.
- Tordoff, H. B. 1959. A condor from the Upper Pliocene of Kansas. Condor, 61:338-343.
- Van den Berge, J. C. 1975. Aves myology. pp. 1802-1848. In R. Getty (ed.) Sisson's and Grossman's The Anatomy of the Domestic Animals. W. B. Saunders, Philadelphia.
- van den Driesch, A. 1976. A guide to the measurements of animal bones from archaeological sites. Peabody Museum of Archeology and Ethnology. Harvard University Bulletin 1:ix + 137 pp. + 62 figs.
- Voorhies, M. 1984. '*Citellus kimbailensis*' Kent and '*Propriophenacomys uptegrovensis*' Martin, supposed Miocene rodents are Recent intrusives. Journal of Paleontology, 58:254-258.
- Vuilleumier, F. 1984. Faunal turnover and development of fossil avifaunas in South America. Evolution, 38:1384-1396.
- Vuilleumier, F. in press. What birds can tell us about continental connections. In F. G. Stehli and S. D. Webb (eds.). The Great American Interchange. Plenum Press, Geobiology Series, New York.
- Warter, S. L. 1976. A new osprey from the Miocene of California (Falconiformes: Pandionidae). Smithsonian Contributions to Paleobiology, 27:133-139.
- Webb, S. D. 1964. The Alachua Formation. 1964 Field trip. Society of Vertebrate Paleontologists Guidebook. Gainesville, Florida. pp. 22-29.
- Webb, S. D. 1966. A relict species of the burrowing rodent, *Mylagaulus*, from the Pliocene of Florida. Journal of Mammalogy, 47:401-412.
- Webb, S. D. 1969. The Pliocene Canidae of Florida. Bulletin of the Florida State Museum, Biological Sciences, 14:273-308.

- Webb, S. D. 1973. Pliocene pronghorns of Florida. *Journal of Mammalogy*, 54:203-221.
- Webb, S. D. 1974. Chronology of Florida Pleistocene Mammals. pp. 5-31. In S. D. Webb (ed.). *Pleistocene Mammals of Florida*. University Presses of Florida, Gainesville.
- Webb, S. D. 1976. Underwater Paleontology of Florida Rivers. pp. 479-481. *National Geographic Society Research Reports, 1968 Projects*, National Geographic Society, Washington, D.C.
- Webb, S. D. 1981. Kyptoceras amatorum, new genus and species from the Pliocene of Florida, the last protoceratid artiodactyl. *Journal of Vertebrate Paleontology*, 1:357-365.
- Webb, S. D. 1983. A new species of Pediomeryx from the late Miocene of Florida, and its relationships within the subfamily Cranioceratiniae (Ruminantia: Dromomerycidae). *Journal of Mammalogy*, 64:261-276.
- Webb, S. D. 1984. On two kinds of rapid faunal turnover. pp. 417-436. In W. A. Berggren and J. A. Van Couvering (eds.). *Catastrophes and Earth History: the new uniformitarianism*. Princeton University Press, Princeton.
- Webb, S. D. in press. Osteology of Thinobadistes Hay, the oldest mylodontid sloth from North America. *Florida State Museum Bulletin, Biological Sciences*.
- Webb, S. D., B. J. MacFadden, and J. A. Baskin. 1981. Geology and Paleontology of the Love Bone Bed from the Late Miocene of Florida. *American Journal of Science*, 281:513-544.
- Webb, S. D. and N. Tessman. 1968. A Pliocene vertebrate fauna from low elevation in Manatee County, Florida. *American Journal of Science*, 266:777-811.
- Weigel, R. D. 1958. Great Auk remains from a Florida shellmidden. *Auk*, 75:215-216.
- Weigel, R. D. 1962. Fossil Vertebrates of Vero, Florida. *Florida Geological Survey Special Publication*, 10:1-59.
- Welty, J. C. 1975. *The Life of Birds*. W. B. Saunders, Philadelphia. 623 pp.
- Wetmore, A. 1931. The avifauna of the Pleistocene in Florida. *Smithsonian Miscellaneous Collections*, 85:1-41.
- Wetmore, A. 1943. Fossil birds from the Tertiary Deposits of Florida. *New England Zoological Club*, 32:59-68.
- Wetmore, A. 1958. Miscellaneous notes on fossil birds. *Smithsonian Miscellaneous Collections*, 135:1-11.

- Williams, K., D. Nicol, and A. Randazzo. 1977. The geology of the western part of Alachua County, Florida. Bureau of Geology, Division of Natural Resources, Florida Department of Natural Resources, Report of Investigations No. 85:1-98.
- Wolff, R. G. 1973. Hydrodynamic sorting and ecology of a Pleistocene mammalian assemblage from California (U.S.A.). *Paleogeography, Paleoclimatology, and Paleoecology*, 13:91-101.
- Wolff, R. G. 1975. Sampling and sample size in ecological analyses of fossil mammals. *Paleobiology*, 1:195-204.
- Wolff, R. G. 1978. Function and phylogenetic significance of cranial anatomy of an early bear (Indarctos), from Pliocene sediments of Florida. *Carnivore*, 1:1-12.
- Wood, D. S. 1979. Phenetic relationships within the family Gruidae. *Wilson Bulletin*, 91:384-399.
- Wood, D. S. 1983. Phenetic relationships within the Ciconiidae (Aves). *Annals of the Carnegie Museum*, 52:79-112.
- Wood, D. S. 1984. Concordance between classifications of the Ciconiidae based on behavioral and morphological data. *Journal Ornithologie*, 125:25-37.
- Wood, H., R. Chaney, J. Clark, E. Colbert, G. Jepson, J. Reeside, and C. Stock. 1941. Nomenclature and correlation of the North American continental Tertiary. *Bulletin of the Geological Society of America*, 52:1-48.
- Woolfenden, G. E. 1959. A Pleistocene avifauna from Rock Spring, Florida. *Wilson Bulletin*, 71:183-187.
- Woolfenden, G. E. 1961. Postcranial osteology of the waterfowl. *Bulletin of the Florida State Museum, Biological Sciences*, 6:1-129.
- Wright, D. B. and S. D. Webb. 1984. Primitive Mylohyus (Artiodactyla: Tayassuidae) from the late Hemphillian Bone Valley of Florida. *Journal of Vertebrate Paleontology*, 3:152-159.
- Wyles, J. S., J. G. Kunkel, A. C. Wilson. 1983. Birds, behavior, and anatomical evolution. *Proceedings of the National Academy of Sciences, U.S.A.* 80:4394-4397.
- Zusi, R. L. and R. W. Storer. 1969. Osteology and myology of the head and neck of the Pied-Billed Grebe (Podilymbus). *Miscellaneous Publications, Museum of Zoology, University of Michigan*, 139:1-49.
- Zusi, R. L., D. S. Wood, and M. A. Jenkinson. 1982. Remarks on a world-wide inventory of avian anatomical specimens. *Auk*, 99:740-757.

BIOGRAPHICAL SKETCH

Jonathan J. Becker was born in Jerome, Idaho, on 16 December 1955 and was raised on a nearby farm. He graduated from the Jerome High School in May 1974 and attended Idaho State University in Pocatello, Idaho, from 1974 to 1980; receiving a B. S. in zoology with high honors in May 1978 and a M. S. in zoology/biology in May 1980. Since August 1980 he has attended the University of Florida, graduating with a Ph.D. in zoology in August 1985. He is currently a postdoctoral fellow at the National Museum of Natural History, Smithsonian Institution.

He is a member of the American Association for the Advancement of Science, American Ornithologists' Union, American Society of Mammalogists, Biological Society of Washington, Cooper Ornithological Society, Florida Academy of Science, Sigma Xi, Society of Systematic Zoology, Society of Vertebrate Paleontology, and Wilson Ornithological Society.

His current research interests include the functional morphology of birds and mammals and the evolution, systematics, and biochronology of the Neogene birds of North America.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Pierce Brodkorb

Pierce Brodkorb, Chairman

Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Richard A. Kiltie

Richard A. Kiltie
Assistant Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

S. David Webb

S. David Webb
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Ronald G. Wolff

Ronald G. Wolff
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Elizabeth S. Wing

Elizabeth S. Wing
Professor of Anthropology

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School, and was accepted for partial fulfillment of the requirements of the Doctor of Philosophy.

August 1985

Dean for Graduate Studies and Research